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MOURNING WARBLER *(Oporornis philadelphia).*
Male at nest with young. Photographed by Hal H. Harrison.

A LIFE HISTORY OF THE MOURNING WARBLER

BY GEORGE W. COX

DURING the summers of 1956 and 1957 I studied the breeding biology of the Mourning Warbler (*Oporornis philadelphia*) at the University of Minnesota Forestry and Biological Station in Itasca State Park, Minnesota. Here, in contrast to much of the breeding range of the species, the Mourning Warbler is one of the commoner nesting warblers. During the spring of 1957 I made observations on migrating Mourning Warblers at Urbana, Illinois. In February, March, and April, 1959, I made scattered observations of the species in its winter range in the Panama Canal Zone. Since no comprehensive life history study of this species has been published, an attempt is made here to summarize available information related to the aspects of the breeding biology investigated in the present study.

ACKNOWLEDGMENTS

This paper is based on a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at the University of Illinois, Urbana, Illinois.

I express appreciation to S. Charles Kendeigh, who directed the study, and to John T. Emlen, Jr., and Wilbur Mayhew who offered valuable suggestions during the course of it. William Marshall and T. Shantz-Hansen kindly made facilities of the University of Minnesota Forestry and Biological Station available to me, and M. Moynihan and Richard Brewer offered valuable suggestions regarding the manuscript. Finally, sincere thanks are extended to W. D. Stull for guidance both during the course of the study and during the writing of the paper.

METHODS

During the summer of 1956 three nests (#1, #2, #3, 1956) were studied from blinds situated close to the nests. In 1957 two additional nests (#1, #2, 1957) were studied, one with the aid of an itograph, a device for automatically recording visits to the nest by the parents. This itograph was a modification of the type used by Hann (1937), and consisted of a hardware-cloth cage fitted over the nest, and a battery-run recorder located in a nearby blind. The cage over the nest had a single opening through which the parents entered and left. The record obtained, however, did not distinguish between birds entering or leaving. Because of this, difficulties of interpretation were encountered. During incubation these difficulties were greatly reduced by the observer frequently visiting the blind and marking on the record whether the female was on the nest or not, thus providing reference points for interpreting adjacent records of entrance or departure of the parents. After the young had hatched and both parents were actively feeding the young, as well as the female brooding for longer periods of time, interpretation was more difficult. For this reason data from this period are more approxi-

mate, and have been summarized separately from data obtained from direct nest observation.

During both summers observations were also made on the behavior and ecology of the pairs with nests under observation and of other territorial pairs throughout the park.

Range and Migration

The breeding range of the Mourning Warbler extends, in the north, from west-central Alberta eastward through central Saskachewan and Manitoba, northern Ontario, and central Quebec to Newfoundland and Nova Scotia, and in the south, from northeastern North Dakota eastward through the northern parts of Minnesota, Wisconsin, and Michigan to northern Pennsylvania and southern New York, with a southward extension in the mountains to West Virginia (for detailed account, see A.O.U., 1957). In the southern extension of the range the species breeds only at higher elevations. In Massachusetts it occurs mostly above 1600 feet, although occasionally as low as 940–960 feet (Eliot, 1941). In western Pennsylvania the lower limit is about 1100 feet (Todd, 1940). In West Virginia (Brooks, 1940) and Maryland (Stewart and Robbins, 1947) the 3000-foot contour is the lower limit of the species.

The winter range, although poorly known, seems to extend from southern Nicaragua to Colombia, western Venezuela, and northern Ecuador (A.O.U., 1957). In the Panama Canal Zone, from February to April, 1959, I found the species to be a not uncommon winter resident in the lowland areas from sea level to about 500 feet. During this period the species was observed five times in edge areas with dense brush or tall rank grass. Miller (1947) reports that in the Magdalena Valley of Colombia they frequented low tangles and understory vegetation in damp woodlands. In Costa Rica Skutch (in Bent, 1953) states that low dense thickets and fields overgrown with tall weeds and rank grass are favorite habitats. He states that he has observed them mainly in the lowlands up to 4000 feet, but that they are still one of the commoner wintering warblers at 3000 feet.

The migration route of the species is primarily through Central America (Stevenson, 1957). In general it is one of the later migrants, leaving the winter range in March and April (Bent, 1953) and arriving at the latitude of Champaign, Illinois, and central and northern Ohio about May 11 or 12 (Smith, 1930; Jones, 1914; Borror, 1950). Observations of Soper (1949) and Peters and Burleigh (1951) at the extremities of the breeding range indicate that the species has reached most of this area by the last week in May.

At Urbana, Illinois, during the spring of 1957, 48 individuals of this species were observed between May 10 and May 25. The majority were ob-

served in brushy edges, thickets and understory vegetation in open woods. When first noted, 90 per cent of the birds were in vegetation less than 5 feet in height.

In fall, migration begins early, with immature birds often appearing far south of the breeding range in early August, as, for instance, in Texas on August 4 (Baumgartner, 1951). At Chicago the average fall arrival is about August 25 (Clark and Nice, 1950), and in central Ohio the first birds appear about September 5 (Borror, 1950). Arrival in the winter range occurs during the last half of September and the first half of October (Bent, 1953).

Breeding Habitat

The Mourning Warbler is found in a variety of habitats, including brushy woodland clearings (Gromme, 1938; Saunders, 1938; Forbush, 1929; Peters and Burleigh, 1951), forest edges, brushy edges of marshes and bogs (Roberts, 1932), and dense second growth (Roberts, 1932; Todd, 1940; Brooks, 1940). In the present study area, Hickey (1956) found the species strongly associated with clearings, while Kendeigh (1956) noted it most strongly associated with aspen-birch stands.

During the summer of 1957 I obtained data on the general habitat of the species by spot-checks of areas occupied by singing males throughout the park. Males were found in all the major vegetation types, from almost pure stands of red, white, or jack pine to stands of maple-basswood, spruce-fir, aspen and aspen-birch. In most cases these males were associated with edge conditions such as road edges, logging trails, bog borders, clearings, or areas of open woods. Occasionally, however, they were noted where well defined edge conditions seemed to be absent.

The vegetational characteristics of four territories were determined by quantitative measurements of tree density, degree of canopy closure, and type of ground cover. Canopy closure and ground cover were measured by walking parallel line transects 50 feet apart through each territory and counting the number of paces through each condition (open or closed canopy, herbs, shrubs or bare ground). Data on tree density were obtained by a method of stratified random sampling, using 30- by 30-foot quadrats laid out in a manner described by Oosting (1956:50). In these quadrats all trees more than two inches dbh were identified and measured. From these data the number of stems per acre, and the average diameter and the average basal area for each species and each territory were computed.

Canopy closure in these territories varied from 48 to 77 per cent (Table 1). Ground coverage by herbs varied from 41 to 81 per cent and by shrubs from 18 to 59 per cent. These results and a consideration of the features common

TABLE 1

CHARACTERISTICS OF FOUR MOURNING WARBLER TERRITORIES AT ITASCA STATE PARK

	1	2	3	4
Territory size (acres)	1.7	2.2	1.8	1.6
Herb coverage (per cent)	65	43	41	81
Shrub coverage (per cent)	34	53	59	18
Bare ground (per cent)	1	4	0	1
Canopy closure (per cent)	77	48	71	69
Trees per acre	334	211	281	358
Average tree dbh (inches)	7.5	6.3	7.3	8.4
Basal area per acre ($ft.^2$)	111.6	51.6	111.7	159.2
Per cent basal area of deciduous species	68	98	18	7
Per cent basal area of coniferous species	32	2	82	93

to the various other locations in which the Mourning Warbler was noted in the park, and to other habitats from which it has been reported, suggest requirements for a partially open canopy and the presence of both herb and shrub cover on the ground. If these requirements are satisfied the species may occur in a wide range of plant communities ranging from almost pure coniferous (Territories 3 and 4, Table 1) to pure deciduous (Territories 1 and 2) and even in relatively dense coniferous forests, provided there are scattered openings.

COMPETITION WITH ASSOCIATED SPECIES

On the biological station grounds at Itasca Park, where five territories of the Mourning Warbler were under close observation during the summer of 1957, 11 other species of warblers held territories which overlapped with those of Mourning Warblers. These were the Blackburnian (*Dendroica fusca*), Black-throated Green (*Dendroica virens*), Parula (*Parula americana*), Chestnut-sided (*Dendroica pensylvanica*), Black-and-white (*Mniotilta varia*), Nashville (*Vermivora ruficapilla*), Myrtle (*Dendroica coronata*), and Golden-winged (*Vermivora chrysoptera*) Warblers, American Redstart (*Setophaga ruticilla*), Yellowthroat (*Geothlypis trichas*), and Ovenbird (*Seiurus aurocapillus*). Interspecific aggressive behavior was noted with only two of these, the Yellowthroat and the Chestnut-sided Warbler.

On four occasions (one in migration at Urbana, Illinois) encounters were noted between male Mourning Warblers and Yellowthroats (both sexes). These encounters involved mutual wing-flipping and tail-flipping displays,

usually accompanied by *tshrip* notes (see section on vocalizations), and occasionally chases. The aggressive behavior on the part of the male Mourning Warbler was similar to that shown in encounters with other Mourning Warblers.

Several authors have pointed out the similarity of the habitats of the Mourning Warbler and the Yellowthroat (Roberts, 1932; Todd, 1940). On the biological station grounds at Lake Itasca, Yellowthroat territories overlapped all five of the Mourning Warbler territories studied there, and two of the Yellowthroat nests were known to be located inside Mourning Warbler territories. There was no evidence of mutual exclusiveness of territories.

One example of aggressive behavior was noted between the Mourning Warbler and the Chestnut-sided Warbler. On June 19, 1957, in an area where territories of the two species overlapped, the male Mourning was observed to chase the male Chestnut-sided briefly. In the same area, these same two birds were observed singing in a clump of shubbery where the nest of the Chestnut-sided was located. At this time the male Mourning Warbler gave a series of soft, gurgling phrases rather than the typical territorial song. There was no evidence of mutual exclusiveness of territories between these two species either, and on the biological station grounds the territory of one pair of Mourning Warblers almost completely overlapped that of a pair of Chestnut-sided Warblers.

Food Habits

Few food habits data are available for this species. In eight stomachs of adult Mourning Warblers from the vicinity of Lake Nipagon, Ontario, Kendeigh (1947) found that spiders, various beetles, and Lepidoptera constituted over 50 per cent of the contents. Other insects typical of the ground and low vegetation were present in smaller amounts. Saunders (1938) and Roberts (1932) report that nestlings are fed mainly on Lepidoptera larvae. This item was commonly brought to the young in the present study, but numbers of other small insects were fed as well.

Relation to Predators

Two of the nests under observation during 1956 fell victim to predators. One, from which eggs were taken, was in an area frequented by two ground squirrels (*Citellus tridecemlineatus* and *C. franklini*), the eastern chipmunk (*Tamias striatus*), the least chipmunk (*Eutamias minimus*), and the red squirrel (*Sciurus hudsonicus*) by day and the racoon (*Procyon lotor*) by night. The nest itself was little disturbed and it seemed likely that one of the smaller mammals was responsible. The second nest, from which nestlings

were taken, was located in an area frequented by red squirrels and least chipmunks. This nest was also little disturbed, suggesting the action of one of these small mammals.

On one occasion, where Mourning Warblers had young just out of the nest, the parents, several Blue Jays (*Cyanocitta cristata*), and several Red-eyed Vireos (*Vireo olivaceus*) were found scolding a large hawk or owl. The Mourning Warblers remained in the dense underbrush and gave loud *tshrip* notes.

Two types of distraction displays were given by the adults in response to the observer approaching the nest or the young birds after they had left the nest. When a nest containing eggs or young was approached the female usually remained on until the observer was quite close. She would then dive quickly over the edge and run away quickly through the ground vegetation, not taking flight until reaching a distance of 20–25 feet from the nest. This escape was very mouse-like, and often a peculiar gait seemed to be used. This behavior may well function as a distraction display based on the resemblance of the female to a mouse scurrying through the leaves, since the action, *per se*, is conspicuous, but the identity of the female as a bird may not be evident. This type of behavior has also been noted by Forbush (1929) and Gromme (1934).

A typical "broken wing" display was also given by the adults, especially during the period just after the young had left the nest. The initial part of the display was most intense. The adults would dash and flop through the ground vegetation, flipping the wings outward from the body, and often holding them out in a dragging position for short periods. During this display *tsip* notes were usually given. This behavior became weaker as the young birds grew older, but was noted for about two weeks after the young had left the nest. In the present study this behavior was noted occasionally during the period when the young were still in the nest. Gromme (1934) recorded this display during incubation, also.

The Mourning Warbler is not uncommonly a victim of the Brown-headed Cowbird (*Molothrus ater*). During the present study one nest was parasitized, containing one egg of the parasite and three of the host. Twelve other instances of parasitism have been reported in the literature, including five (Pitelka, 1939; Roberts, 1932; Lloyd, 1949; Chambers, 1947; Hickey, *et al.*, 1955) not included in summaries by Friedmann (1929, 1931, 1938, 1949).

Vocalization

In the following discussion the term "song" is applied to the more complex vocalizations and the terms "call notes" or "notes" to the less complex. These should be understood as simply convenient names for these vocaliza-

tions and not as interpretations of function or motivation. Likewise, the term "territorial song" refers to the complex male vocalization which may be similar in function and motivation to the advertising songs of other species.

The territorial song of the Mourning Warbler is loud and ringing, with a somewhat throaty quality. It consists of 3–7 two-parted phrases, with the accent on the first syllable of each phrase. Typically, the last 1–3 phrases are given on a lower pitch. The length of the song varies approximately from 1–1¾ seconds (Gunn and Borror in Griscom and Sprunt, 1957). A typical song of the males in the present study area could be paraphrased *whee-o whee-o whee-o, whoo-e whoo-e.* Other common song patterns are given by Gunn and Borror (*op. cit.*). Variations I noted consisted of differences in number of phrases, omission of the changed ending, and differences in pitch and quality.

Only the male sang. He showed definite attentive and inattentive song periods, the latter being devoted mainly to feeding. Attentive periods were long, often over an hour in length, but within these the rate of singing varied. The rate of singing varied from 1–8 songs per minute, averaging about 3.6, giving an interval of about 15 seconds between songs. At times feeding and singing were carried out together in the underbrush, and during these times the rate of song was low (1–2 per minute). High intensity singing (6–8 per minute) was usually noted after territorial encounters.

The height in the vegetation at which territorial song was given varied from near ground level to about 40 feet high in trees. The stratum with the most records (37 per cent of 1200 records) of singing birds was that of low underbrush less than 5 feet in height. The stratum of second highest number of records was that between 20 and 25 feet (22 per cent). At this level the males often perched for long periods and sang rather steadily. The heights of those perches at which males remained and sang steadily for at least 10 songs ("singing perches"), were most frequently between 20 and 25 feet. Kendeigh (1947) found nearly the same distribution of song in relation to height in the vegetation in Ontario, where he noted the average height to be 26 feet, with some as high as 60 feet. Roberts (1932) and Forbush (1929) have also noted the tendency of the males to sit motionless at certain perches, singing steadily for long periods. When disturbed from these perches the males usually flew quickly into the underbrush, frequently to continue singing there.

A definite pattern of movement was followed during the attentive periods of song. At the beginning the male would fly up to a low branch, give a few songs, fly to a higher perch nearby, give a few more songs, and continue this process until reaching a perch 20–30 feet high, from which he would sing steadily for a long time (often 40–50 songs). From here occasional

flights would be made to adjacent trees, or back down into the underbrush, in which case the performance would often be repeated. Trautman (1940) has described this behavior in Ohio in migration.

In the present study singing was less frequent in the afternoon hours. In New Hampshire, Wright (1913) stated that song began about 37 minutes before sunrise. Trautman (1940), however, states that males in migration at Buckeye Lake, Ohio, remained silent during the early morning warbler chorus.

Song declined near the end of the nesting cycle, but did not cease until some time after the young were out of the nest. Roberts (1932) found young awing in late July with the parents still in full song. Saunders (1948*a*) found the average date of song cessation to be July 16 in Allegany Park, New York. He also noted a revival of song, frequently the flight song, between August 5 and 16 (Saunders, 1948*b*).

At Urbana, Illinois, in the spring of 1957, migrating males were frequently heard singing. One male was observed to maintain a nearly constant rate of 3–4 songs per minute for almost an hour. Trautman (1940) on one occasion observed 25 males singing at one time in migration in Ohio. Song is rare during fall migration.

The male also possesses a flight song, which is given as the bird flies upward, and ceases when a certain height is reached (Saunders, 1954). At Itasca Park the entire performance was never seen, but was heard on many occasions. Although hard to describe because of its rapidity, the song apparently begins with a series of chipping notes, followed by a rapid version of the territorial song, and ends with a few more chipping notes. A paraphrase of this song might be given as: *chi-chi-chi-chip-chip-cheery-cheery-chorry-chorry-chi-chip*. This song was heard once in mid-afternoon in migration at Urbana, Illinois. At Itasca Park it was heard between June 21 and July 13, but was most common during the first part of July when most pairs were in the latter stages of nesting. It was given at various times throughout the day. On one occasion it occurred at the beginning of a period of territorial song. In the territory of one of the pairs whose nests were under observation the flight song was heard on three occasions during the period when this pair had nestlings or fledgings. The sex of the bird giving this song was noted only twice; it was the male.

A third type of song pattern was heard once in early June. A male gave a soft, patternless series of muttering notes, interspersed with notes resembling soft *tschrip* notes. The significance of this song was not determined.

Two call notes were given by the adults. One was a *tshrip*, loud and rather harsh in quality. It was heard commonly interspersed with the territorial song of the male, and was also frequently noted in both male and female when

disturbed by an observer away from the nest area. It was heard commonly from migrating birds. It may have had some signal function between the male and female, since during the period of incubation, when the male occasionally fed the female, it was noted in association with this behavior (see section on incubation).

The second note, a *tsip*, less harsh, and higher in pitch, was heard commonly when I approached a nest containing eggs or young, or when the young fledglings were approached. It was also given during a territorial encounter between two females.

Territories and Territorial Defense

The sizes of ten territories were measured during the summer of 1957. The boundaries of these territories in early June were determined by marking the locations of singing males in the field. At least four hours of observation were spent with each pair, divided among at least three trips. Lines connecting the outermost points, thus giving the maximum enclosed area, were measured with a steel tape, and the direction of these lines noted with a compass. These measurements were then transferred to a map, and the enclosed area measured by dividing the areas into triangles and calculating their sizes.

The ten territories ranged in size from 1.6 to 2.4 acres, averaging 1.9 acres. Near Lake Nipagon, Ontario, Kendeigh (1947) found that during a spruce-budworm outbreak two territories were 0.9 and 1.5 acres in size. Kendeigh (pers. comm.) has suggested that these measurements were probably not as detailed as those of the present study, rather than representing a response to the spruce-budworm outbreak. In New Hampshire the foraging area of a pair was about 1.5 acres (Wallace, 1949).

The territories observed at Itasca Park included the nest site, and were used as foraging areas by the parents.

Two males, studied closely in 1957, defended the entire territory by territorial song early in the nesting cycle, but in the later stages their singing was confined to a smaller portion of the territory. In the period between June 20 and 25 the male of a nest containing nestlings confined his singing to two small areas near the nest, while a second, during the same period, sang regularly only in a small area at the opposite end of the territory from its nest, which contained eggs. Although singing seemed to be confined chiefly to these small areas, territorial encounters were noted in other parts of the territory, suggesting that the entire area was defended against other birds if they were noticed.

In 1957, when the nest sites of only two pairs were known, the males did not

sing in the immediate vicinity of the nest. The closest the two males sang to their nests was 30 feet and 85 feet.

In addition to song, other more aggressive displays were used to defend the territory against intruding Mourning Warblers. Good observations on these encounters were made on only three occasions. One encounter, in June, 1956, took place between two males in thick underbrush. The males hopped rapidly from perch to perch, bobbing their bodies violently. At the same time they rapidly flipped their wings outward and rapidly opened and closed their tails. Frequent *tschrip* notes were given. Occasionally short winding chases through the brush were made. During this encounter, the female of one pair appeared and began begging from the male by fluttering her wings and gaping. After a few minutes the males separated, one beginning to sing rapidly, the other continuing to give *tshrip* notes. After a few more minutes the second male also began to sing. During late June, 1957, a similar encounter was noted between two other males. During July, 1957, an encounter taking place mainly between two females was seen. At this time both pairs had fledglings, and the encounter was probably caused by the movement of one group into the territory of the second. When first seen, both females were in a small tree, and were both giving *tsip* and *tshrip* notes. Bobbing and wing- and tail-flipping similar to that seen in encounters between males were also performed. The two birds gradually hopped higher in the tree, then flew quickly down into the underbrush and engaged in a short, winding chase. Following this they returned to the same tree and repeated the posturing behavior. Both males remained nearby in the undergrowth, giving *tshrip* notes. This encounter continued for over an hour.

Territorial behavior was evident in some migrant birds at Urbana, Illinois. Between May 16 and 24, 1957, a male Mourning Warbler was found daily in a brushy area adjacent to a small stream. On the basis of song pattern I judged this to be the same bird each day. This bird sang regularly in an area about an acre in size. No encounters with other males were noted.

Time of Nesting

Five nests were found during the course of the present study. The following summary indicates the general course of events at these nests:

No. 1, 1956. Found on June 14, 1956, containing three eggs. A fourth added the next morning. Eggs removed by a predator late in incubation.

No. 2, 1956. Found on June 21, 1956, with three eggs of the owner and one of the Brown-headed Cowbird (latter I removed). Two of the eggs hatched on July 3 (other infertile) but the young later died when they fell from the poorly constructed nest (Cox, 1958).

No. 3, 1956. Found on July 1, 1956, with three eggs which hatched on July 6. The young were later removed by a predator.

No. 1, 1957. Found on June 12, 1957, containing five eggs, one of which disappeared during incubation. The young hatched on June 20 and left the nest on June 28.

No. 2, 1957. Found on July 5, 1957, with four well developed young which left the nest before noon of the following day.

Data on time of nesting in this species are scant. The earliest observed date of a nest with eggs is May 31 (Macoun and Macoun, 1909) in southern Ontario, and the latest is July 15 in Minnesota (Roberts, 1932). The earliest observed date of a nest with young is apparently June 20 in Minnesota (present study), and the latest, July 17 in Minnesota (Chambers, 1947).

Nest Site

Nests of the Mourning Warbler are usually placed on or close to the ground. In the present study, four of the nests rested on the ground surface and one was supported on fallen branches 5½ inches above the ground. Records in the literature are mostly of nests on the ground or a few inches above it. The highest record is of a nest 30 inches off the ground (Roberts, 1932).

The nests are concealed in dense herbaceous or shrubby vegetation in most cases. In the present study, three nests were hidden in dense low herbs of the forest floor, one in dense tall grass in a small forest opening, and one in a dense growth of raspberry (*Rubus* sp.) at the edge of an area covered with this plant. The nests are usually supported laterally by stems of the concealing vegetation.

In the literature nests are usually reported from edge areas such as woodland edges or clearings, logging trails, or edges of bogs and marshes. Tree density and coverage of herbs and shrubs were measured in the vicinity (40-foot radius) of the five nests located in the present study. At these sites the average basal area and the number of stems per acre of trees were noticeably lower than in the previous analysis of the territories as a whole (Table 2). This suggests that at least in an area where the territories of the species are located in woodland which is fairly well developed the nests are placed in a more open part of the territory.

Nest Structure and Composition

Nests of this species are rather bulky. Measurements for the five nests in the present study, together with five others reported in the literature (Roberts, 1932; Todd, 1940; Davison, 1891; Bent, 1953) gave average figures of 89 mm. (range 70–102 mm.) for outside height, 130 mm. (range 90–229 mm.)

for outside diameter, 47 mm. (range 38–57 mm.) for inside depth, and 54 mm. (range 44–64 mm.) for inside diameter.

Nests vary widely in composition, depending on the nature of available materials, but are usually described as consisting of leaves, weed stalks, pieces of bark, grasses and sedges, with a lining of fine rootlets, grasses or hair. In the nests I studied leaves were always present, usually as the outer shell of the nest, and varied according to the type available in the vicinity of the nest. Grasses, weed stems, and fibrous tree bark were used to bind the wall together. Linings were of fine weed stems, fine rootlets, grasses, and fine strips of bark.

Weights of four of the nests which had been air-dried for at least two weeks were 11.6, 20.2, 22.6, and 28.0 grams; a nest found by Walkinshaw (1956) weighed 12.2 grams.

TABLE 2

COMPARISON OF TERRITORIES AND NEST SITES* WITH RESPECT TO TREE DENSITY AND GROUND COVER

	Basal area per acre	Stems per acre	Per cent shrub coverage	Per cent herb coverage	Per cent bare
Territories (4)	108.5 ft.^{2}	296	41	58	1
Nest sites (5)	76.5 ft.^{2}	219	42	55	3

*40-foot radius of nest

EGGS AND EGG LAYING

Clutch sizes in the present study were 3, 3 (parasitized by cowbird), 4, 4 (brood size), and 5. The average size for these and for 31 other clutch sizes taken from the literature was 3.7, with a variation from 2–5.

In a single observation of the time of laying, the last egg of nest # 1, 1956, was laid between 3:15 and 6:15 a.m.

INCUBATION

Hofslund (1954) recorded the length of the incubation period of one pair of Mourning Warblers as 12 days, with the same probable time for a second nest. In the present study, nest # 2, 1956, was found on June 21, and contained a full clutch of three eggs at that time. On July 3, 12 days after the nest was found, the young hatched, indicating a minimum period of 12 days for this nest.

The female may begin incubation before the clutch is complete. At nest # 1, 1956, which was found with an incomplete clutch, the female was

observed on the nest three of the four times it was visited on the day before laying of the last egg.

The female usually approached and left the nest by hopping through the ground vegetation for 10–30 feet, and was never observed to fly directly to the nest. Definite routes of approach to and departure from the nest were used, especially in the immediate vicinity of the nest. On arriving at the nest the female usually paused on the rim and looked into the nest cavity for a few seconds, after which she entered the cavity and settled with a side-to-side rocking motion, spreading the feathers on either side of the brood patch as she did so.

While on the nest the female engaged in various activities such as resettling, preening, particularly around the brood patch, pecking at materials in the nest bottom, and moving the eggs. Occasionally she would "yawn," briefly close her eyes, or tuck her bill under her wing for a few seconds. During hot periods of the day, or when direct sunlight fell on the nest, she would sit with the bill agape, "panting" almost constantly.

Little or no response was shown to loud calling of other birds at distances over 50 feet from the nest. When other birds or small mammals passed through the vegetation within 5 or 6 feet of the nest, the female usually elevated her head and looked in the direction of the disturbance.

During incubation the female is fed by the male both at and away from the nest. On June 14, 1956, the female of nest # 1 was seen to fly up from the vicinity of the nest to a perch about 5 feet off the ground in a small spruce. The male appeared and the female begged by gaping, fluttering her wings, and uttering soft, throaty, musical sounds barely audible to the observer 50 feet away. The male fed her and flew down to the ground, *tshrip*-ping vigorously. He then flew back up and fed the female twice more. Following this he gave *tshrip* notes from several perches and flew away. The female flew down into the ground vegetation and returned to the nest.

Several times while the observer was watching the incubating female of this same nest from a blind, the male came near the nest and began giving *tschrip* notes. In several instances the female responded by giving similar notes from the nest but did not leave. This response occured on the average 7.4 minutes after the beginning of an attentive period of brooding by the female (attentive periods averaged 28.2 minutes for this bird). On four occasions when the male appeared and gave *tschrip* notes near the nest the female responded by giving similar notes from the nest and then leaving the nest in less than a minute. The attentive periods terminated by this behavior averaged 13.5 minutes in length, seeming to indicate that these periods were shortened by the appearance of the male and that possibly they also represented times when the male fed the female away from the nest. It is suggested

that the relative strength of the incubation drive (higher when occurring shortly after the beginning of an attentive period, lower later) to the drive activated by the appearance of the male was the controlling factor in whether the female left the nest or not.

The male also fed the female on the nest. This was difficult to observe because of the extreme shyness of the male. When approaching the nest the male occasionally gave low *tshrip* notes, but often appeared silently. The food item brought was most frequently a large green larva. When the male appeared the female either remained in the nest cavity or backed off to the opposite edge of the nest and begged by gaping, spreading her wings slightly and giving soft musical notes. After feeding the male usually remained on the edge of the nest for a few seconds. Sometimes the male apparently followed the female to the nest at the end of an inattentive period to feed her, but this was never seen in entirety. In one instance the female hopped to the edge of the nest with her bill agape, making soft musical sounds. The male was heard giving soft *tshrip* calls in the nearby vegetation, but was apparently frightened by the observer and left.

The function of this behavior may be partly that of anticipatory food bringing as described by Nolan (1958), but since the female was also fed away from the nest, an additional function, perhaps related to the pair bond, is probably involved.

Toward the end of attentive periods of incubation, the female exhibited what might be termed incubation restlessness. From seven to eight minutes before the end of the period the female would begin to shift position and resettle more frequently. From one to four minutes before leaving she would begin to show nervous turning and tilting movements of the head. This behavior became more and more frequent until she left the nest.

The length of the attentive periods in the three nests studied averaged 35.8 minutes, and ranged from 2–93 minutes (Table 3). In respect to the individual females the average lengths were 60.5, 28.2, and 38.4 minutes.

Inattentive periods averaged 9.6 minutes for all three birds together, and 17.8, 8.7, and 9.2 minutes for the three individual females. In these three birds longer average length of attentive periods was correlated with longer average length of inattentive periods.

Length of attentive and inattentive periods also varied with time of day, probably due to daily changes in temperature. Attentive periods averaged longer in the early morning and evening than in mid-day (Table 4). Data on the length of inattentive periods were less conclusive in this regard, but the longest inattentive periods occurred in the afternoon hours.

Overall attentiveness averaged 77.4 per cent and varied only from 76.4 to 81.9 per cent for the individual birds (Table 3). In relation to time of day,

TABLE 3

ATTENTIVE AND INATTENTIVE PERIODS AND OVERALL ATTENTIVENESS DURING INCUBATION FOR THREE MOURNING WARBLERS AT ITASCA STATE PARK

	# 1, 1956	# 2, 1956	# 1, 1957	Total
Attentive periods				
Number	10	45	38	93
Average length (minutes)	60.5	28.2	38.4	35.8
Range (minutes)	18–93	2–52	14–65	2–93
Inattentive periods				
Number	10	45	39	94
Average length (minutes)	17.8	8.7	9.2	9.6
Range (minutes)	9–29	2–17	3–24	2–29
Overall attentiveness				
Time (minutes)	1081	1844	3251	6176
Time in incubation (minutes)	885	1408	2486	4779
Attentiveness (per cent)	81.9	76.4	76.5	77.4

overall attentiveness was highest in the early morning hours and in the evening, and lowest at mid-day (Table 4).

The length of inattentive periods was found to be correlated with the length of the attentive periods immediately preceding them. Longer attentive periods resulted in longer inattentive periods immediately following them (Table 5), probably due to the build-up of a stronger feeding drive. The reverse relation showed no correlation.

TABLE 4

ATTENTIVE BEHAVIOR DURING INCUBATION IN RELATION TO TIME OF DAY*

	4–8 a.m.	8–12 a.m.	12–4 p.m.	4–8 p.m.
No. attentive periods	9	54	13	10
Average length (minutes)	42.6	32.8	37.5	47.7
No. inattentive periods	11	53	14	6
Average length (minutes)	11.1	9.6	12.6	8.5
Total observed time	856	2925	1301	1094
Attentiveness (per cent)	82.9	76.8	74.0	78.6

*# 1, # 2, 1956; # 1, 1957 (see text)

Itograph records from the nest of pair # 1, 1957, during incubation and early feeding of the young gave information on the time of beginning and ending of daily activity by the female. Between June 14 and 26, the female

returned to the nest for the night an average of about 14 minutes before sundown (eight records), with a range of 54 minutes before to 15 minutes after. Two records of departure in the morning were 23 minutes before and 15 minutes after sunrise.

On one occasion the female was seen when returning to the nest immediately after the hatching of one young. When she reached the nest she paused on the rim and pecked in the nest bottom for over a minute, then picked up the broken parts of the egg shell, worked them around with a chewing motion for several minutes, and finally swallowed them.

TABLE 5

LENGTH OF INATTENTIVE PERIODS OF INCUBATION IN RELATION TO LENGTH OF PRECEDING ATTENTIVE PERIODS*

Length of attentive period (minutes)	Number of observations	Average length of following inattentive periods (minutes)
Less than 20	10	6.0
21–30	20	8.4
31–40	23	10.6
41–50	13	12.7
Over 50	9	13.9

*# 1, # 2, 1956; # 1, 1957 (see text)

NESTLING PERIOD

Hofslund (1954) recorded the nestling period in two Minnesota nests as 8–9 days. Cottrille (1958) found that the young left the nest after eight days in one Michigan nest. The young successfully fledged at a known age in only one nest in the present study. In nest # 1, 1957, the first young hatched between 2:10 and 2:25 p.m. on June 20, and the remaining young hatched before 7:30 a.m. on the following day. On the afternoon of June 28 the young left the nest, at an age of between seven and eight days. These young survived and the family group was observed until the young achieved independence.

During this period the adults approach the nest silently. The external stimulus causing the young to gape is therefore tactile and/or visual. Before and shortly after the eyes of the young were open they gaped in response to movement of the nest by the observer. Gaping was seen at irregular intervals when the parents were absent, possibly in response to movements of the other young or to slight movement of the nest by wind. Occasionally the young failed to gape when the parent appeared. In these cases the adult

would hop around the edge of the nest, or back and forth between the nest and an adjacent perch until the young gaped.

After feeding, the adults paused on the edge of the nest for a few seconds. Fecal sacs were expelled by the young during this period. Only the young which had been fed were observed to produce fecal sacs. During the first part of the nestling period the fecal sacs were eaten by the parents. On the seventh day after hatching a fecal sac was carried away from nest # 1, 1957, suggesting that this may be the pattern during the later stages of the nestling period. Production of fecal sacs was lowest in the early morning (Table 7).

The appearance of the male with food while the female was brooding often seemed to result in the female's leaving the nest. In 15 of 27 observations, the female left within two minutes of the arrival of the male. When the female did not leave, she generally would rise and back off to the edge of the nest, often showing begging behavior by gaping in the direction of the male and fluttering her wings. In most cases the male fed the young directly, but he often responded to the female by giving her at least part of the food. On these occasions both would then feed the young.

Sometimes the female did not rise off the nest when the male appeared. When this happened the male usually gave the food to the female who then rose and fed the young. Once, however, the male hopped around the edge of the nest, and when the female rose slightly, fed the young beneath her. Another time, the male fed two young, but still had some food left. The female begged, the male gave the food to her, and she ate it. The female occasionally begged after the male had fed the young and had no food left.

When the food item was large, and the young had difficulty swallowing it, the parents frequently removed the object and reinserted it in the same or a different mouth.

Behavior of the female on the nest during brooding was similar to that shown during incubation. When direct sunlight fell on the nest the female spent much time standing over the young with her wings spread slightly, usually panting.

In direct observations on feeding behavior, the average rate was 2.5 feeding visits per nest per hour during the first four days after the young had hatched. This value ranged from 2.2 to 4.3 per nest per hour in the three nests studied (Table 6). Feeding rate varied with the time of day, the lowest rate being observed in the early morning hours (Table 7). Factors related to this low rate may be high brooding attentiveness in the female, and possibly more active territorial defense by the male at this time.

A fairly complete record of nest activity was obtained with the itograph for the nestling period of nest # 1, 1957. In this record two jogs close together indicated a bird leaving the nest soon after arriving, and were assumed (sup-

TABLE 6

RATE OF FEEDING OF YOUNG IN THREE NESTS OF MOURNING WARBLERS DURING FIRST FOUR DAYS OF NESTLING PERIOD*

	# 2, 1956	# 3, 1956	# 1, 1957	Total
Time observed (minutes)	1172	240	180	1592
Feeding visits by male	26	10	5	41
Feeding visits by female	17	1	8	26
Total feeding visits	43	11	13	67
Feeding visits/nest/hour	2.2	2.8	4.3	2.5
Feeding visits/young/hour	1.2	0.9	1.1	1.1

*Direct nest observations only

ported by observations from the blind while the itograph was recording) to represent a feeding visit. These are summarized in Table 9 as "apparent feeding visits." However, since the female sometimes brought food at the beginning of an attentive period of brooding (represented by a single jog), the total number of feedings could not be determined. Since brooding visits (summarized in Table 9 as "apparent female brooding visits") became less frequent toward the end of the nestling period, the number of "apparent

TABLE 7

BROODING ATTENTIVENESS, RATE OF FEEDING OF YOUNG, AND RATE OF FECAL SAC PRODUCTION DURING FIRST FOUR DAYS OF NESTLING PERIOD IN RELATION TO TIME OF DAY*

	4–8 a.m.	8–12 a.m.	12–4 p.m.	4–8 p.m.
Brooding attentiveness				
Attentive periods	6	26	26	31
Average length (minutes)	20.5	20.5	19.5	14.0
Inattentive periods	6	28	27	34
Average length (minutes)	8.7	8.6	8.0	6.7
Observation time (minutes)	205	805	743	747
Attentiveness (per cent)	71.2	69.4	72.0	63.7
Feeding rate and rate of fecal sac production				
Observation time (minutes)	137	672	627	235
Total feeding visits	2	23	32	10
Feedings/nest/hour	0.9	2.0	3.1	2.6
Feedings/young/hour	0.5	1.2	1.0	1.1
Fecal sacs/young/hour	0.2	0.8	0.7	0.7

*# 2, # 3, 1956; # 1, 1957 (see text)

TABLE 8

BROODING ATTENTIVENESS IN RELATION TO AGE OF YOUNG*

Age (days)	Attentiveness: Observation time (minutes)	Attentiveness: Brooding (per cent)	Duration of attentive periods: Number	Duration of attentive periods: Average length (minutes)	Duration of inattentive periods: Number	Duration of inattentive periods: Average length (minutes)
0	361	68.4	14	17.9	14	7.8
1	1081	63.7	44	15.3	47	8.0
2	690	78.7	24	20.4	26	5.8
3						
4	785	33.1	10	24.2	11	18.2
5	542	37.1	17	11.4	16	16.6
6	308	25.3	7	11.1	7	26.7
7	371	12.1	6	7.7	7	47.1
8	429	3.3	3	4.7	3	135+

*# 2, # 3, 1956; # 1, 1957 (see text)

feeding visits" approximates the true feeding rate more closely at this time. Thus the six-fold increase in the rate of "apparent feeding visits" between the first and eighth days probably represents an increase in the true feeding rate of about four times.

TABLE 9

RATE OF FEEDING OF YOUNG AS RECORDED BY ITOGRAPH FOR NEST #1, 1957, IN RELATION TO AGE OF YOUNG

Age (days)	Time recorded (minutes)	Apparent feeding visits*	Apparent female brooding visits*	Apparent feeding visits/nest/hour	Apparent feeding visits/young/hour
0	405	4	13	0.6	0.2
1	605	17	30	1.7	0.4
2					
3					
4	489	35	4	4.3	1.1
5	226	13	7	3.4	0.9
6	308	30	8	5.8	1.5
7	371	57	7	9.2	2.3
8	429	79	3	11.0	2.8

*See text

Brooding tended to remain high during the first three to four days after hatching, but declined rapidly after this. The length of attentive periods varied between about 15 and 25 minutes during the first four days but decreased rapidly after this (Table 8). Inattentive periods remained short

during the first few days after hatching, and then increased rapidly in length. Overall attentiveness was 63.7 to 78.7 per cent during the first few days and declined to 3.3 per cent on the last day.

Fledgling Period

Observations of the activity of the young after they had left the nest were difficult because their movements were confined to thick underbrush. In addition, the adults usually showed alarm reactions when the family group was approached.

The family group of nest # 1, 1957, was followed for three weeks after it had left the nest on June 28. Although the birds were not marked, confusion with other groups was improbable, since the fledglings from the only close neighbor were of a much different age.

During this three-week period the family group remained within the general area of the territory of that pair, with most of the observations of the group being within 150 feet of the nest site.

When the young left the nest, they were unable to fly, and showed very little development of the tail feathers, By July 4, the tail feathers still showed little development, but the young could fly about 30 feet with a fluttering, uneven flight. On July 12 they were able to fly well and were heard giving weak *tshrip* notes. On July 18, the last day they were seen, they were completely feathered out and were foraging independently, although still accompanied by the adults.

The postnuptial molt of the adults apparently began at about this time. On July 18, two males (one the male from nest # 1, 1957) which were still in company with young birds were just beginning to molt. On July 25, 1957, two females were seen, one in light and one in heavy molt. Dwight (1900) stated that the postnuptial molt occurs in August, but observations of Saunders (1948*a*), with which those of the present study agree, suggest that it begins as early as mid-July.

Summary

The breeding biology of the Mourning Warbler was studied in Itasca State Park, Minnesota, during the summers of 1956 and 1957. Observations on migrants were made at Urbana, Illinois, during the spring of 1957, and on wintering birds in the Panama Canal Zone during the early part of 1959.

In both breeding and winter ranges and in migration the species is a typical inhabitant of forest edge communities. Breeding territories were found in a wide variety of plant communities, where requirements of a partially open canopy and a mixture of herbaceous and shrubby ground cover were satisfied.

Aggressive encounters were noted with Yellowthroats and Chestnut-sided

Warblers, suggesting interspecific competition. Territories of these two commonly overlapped with those of the Mourning Warbler, however.

Vocalizations of the species include a male territorial song, a male flight song, and two call notes in both sexes.

Breeding territories are established and are defended by male song and aggressive displays by both sexes. The average size of the territory is 1.9 acres. The territorial song is given most frequently from low underbrush and from definite song perches 20–25 feet high. The rate of song varies from one to eight songs per minute. It is most frequent in the morning. Song declines during the nesting cycle but does not end until sometime after the young have left the nest. After nesting is well underway the size of the area regularly defended by singing is apparently decreased. Singing was not heard in the vicinity of the nest. A temporary territory was apparently established by a male in migration at Urbana, Illinois.

Nesting was begun mostly in June at Itasca Park. Nests were hidden in thick vegetation on or a few inches above the ground in a more open part of the territory. Leaves, grasses, weed stems, and fibrous bark were the principal items used in nest construction, with fine plant materials used as a lining. Clutch size averaged 3.7 eggs, ranging from two to five. The eggs are probably laid in the early morning. Nest parasitism by the Brown-headed Cowbird is not uncommon. Two nests in the present study were lost to predators, probably small mammals. Two types of distraction displays were shown by the adults when the nests were approached, one possibly based on the resemblance of the female leaving the nest to a small mammal scurrying through the leaves, and the second based on the resemblance of the actions of the adults to those of wounded birds.

Incubation lasts about 12 days, is carried on entirely by the female, and may begin before the clutch is complete. Attentive and inattentive periods averaged 35.8 minutes and 9.6 minutes, respectively, with overall attentiveness averaging 77.4 per cent. Attentiveness was highest in the early morning and evening. The male feeds the female at and away from the nest during incubation. Once the female was observed to eat the egg shell when the young hatched.

The nestling period lasts seven to nine days and the young are fed by both parents. The rate of feeding increases about four times during the period. The rate is lowest in the early morning. Fecal sacs are eaten by the adults at first, but may be carried away later. Brooding by the female is high for the first few days, but decreases rapidly later. The young are unable to fly when they leave the nest, and the family group remains together in the vicinity of the nest for a period of about 2–3 weeks, until the young have achieved independence.

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DEPARTMENT OF ZOOLOGY, UNIVERSITY OF ILLINOIS, URBANA, ILLINOIS, OCTOBER 6, 1959

NEW LIFE MEMBER

S. Dillon Ripley, a member of the Wilson Ornithological Society since 1946, is Director of the Peabody Museum, New Haven, Connecticut. Dr. Ripley received his baccalaureate degree from Yale University, and his doctorate from Harvard University. He is especially interested in avian speciation and ecology, and in waterfowl conservation. From these interests his researches have resulted in the publication of 150 technical papers and bulletins and three books: "Trail of the Money Bird," "Search for the Spring Babbler," and "A Paddling of Ducks." In addition, he is President of the International Council for Bird Preservation, a Fellow of the A. O. U., and a member of Sigma Xi, A. A. A. S., Zoological Society of India, B. O. U., French Ornithological Society, S. African Ornithological Society, etc. The photograph shows Dr. Ripley with an Andean Goose on a private preserve in Litchfield, Connecticut, where he rears waterfowl and other birds.

MASSED WATERFOWL FLIGHTS IN THE MISSISSIPPI FLYWAY, 1956 AND 1957

FRANK C. BELLROSE AND JAMES G. SIEH

ALMOST every year in the Mississippi Flyway there is one waterfowl flight that is greater in scope and magnitude than all others. Some refer to it as the "grand passage" of waterfowl. This great movement usually occurs during the first week of November, but it may be earlier or later. In 1957, this spectacular duck migration occurred from October 23–25; in 1956, it occurred from November 6–8; in 1955, it occurred from October 31 to November 3.

The 1955 grand passage of waterfowl was discussed in an earlier paper (Bellrose, 1957). The present paper largely concerns the grand passage of waterfowl in 1956 and 1957. Although the 1956 and 1957 flights were not so large as the one in 1955, they were still of unusual scope and magnitude in the Mississippi Flyway. They are discussed here not so much because of their size, but primarily because of the unique complementary observations made in Iowa and in Illinois.

The 1955 massed waterfowl flight was well documented on its passage from Canada to Louisiana (Bellrose, 1957). Therefore, in discussing the 1956 and 1957 grand passages of waterfowl we have attempted to provide only a sketchy documentation of the over-all flights in favor of more detailed descriptions of the movement through Iowa and Illinois.

Studies of waterfowl movements are productive of information on three aspects of migration: (1) the mechanics of migration including routes, speed, altitude, and flock behavior; (2) the problem of navigation; and (3) the weather conditions responsible for initiating migratory movements.

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GRAND PASSAGE OF 1956

Extensive Observations.—The prelude to the 1956 grand passage began late in the afternoon of November 5, when at Bismarck, North Dakota, C. H. Schroeder (letter, July 29, 1957) of the Game and Fish Department reported scattered flocks of ducks flying southward. Before sunrise on November 6,

Schroeder heard ducks flying overhead, and at daylight he observed a "sky full of ducks," moving southeast. Most of the ducks were Mallards (*Anas platyrhynchos*), but flocks of Pintails (*A. acuta*), Gadwalls (*A. strepera*), Green-winged Teals (*A. carolinensis*), Shovelers (*Spatula clypeata*), Lesser Scaups (*Aythya affinis*), Canvasbacks (*A. valisineria*), Ring-necked Ducks (*A. collaris*), Redheads (*A. americana*), Buffleheads (*Bucephala albeola*), and Ruddy Ducks (*Oxyura jamaicensis*) also were observed.

W. G. Leitch of Ducks Unlimited telegraphed that on the morning of November 6, 1956, there was an appreciable movement of ducks through and out of southern Manitoba.

At Fergus Falls, Minnesota, Joseph Hopkins (letter, March 11, 1957), U. S. Game Management Agent, reported a mass migration of ducks, which appeared about 11:00 a.m. (C.S.T.) on November 6. The flight was still in progress at sunset. Late in the afternoon many Mallards dropped out of the passing throng to alight on local lakes. On the morning of November 7, Hopkins observed numerous high flying flocks of ducks heading south-southeast whenever there was a break in the low overcast. Several flocks of Whistling Swans (*Olor columbianus*) were observed migrating at a high altitude. The waterfowl flight continued through the afternoon and was still in progress at dark.

There was no indication of the mass migration in the area of Minneapolis, Minnesota, until 9:00 a.m. (C.S.T.) on November 7. At that time, J. D. Smith (letter, August 15, 1957) and others of the U. S. Fish and Wildlife Service noticed long strings of Mallards passing over that city, heading in a southeasterly direction. The flight continued until between 3:30 and 4:00 p.m. In the morning and early afternoon, duck flocks were observed at 3- to 5-minute intervals. Later in the afternoon, however, flocks passed by at intervals of 10 to 15 minutes. Most of the duck flight occurred at about 2000 feet, but during the afternoon the flight dropped progressively lower until by 3:30 p.m. the flocks were at 800 to 1000 feet.

Similar observations were made at Swan Lake, near New Ulm, Minnesota, 60 miles southwest of Minneapolis. There, W. G. Hoerr, local duck hunter, reported (letter to A. H. Hochbaum, January 21, 1957) that ducks showed up from the northwest about 9:00 a.m. on November 7. From that time until 3:30 p.m., when the flight ceased, Mr. Hoerr could see large flocks of ducks through breaks in the clouds and/or when the snow abated. The flight consisted mostly of Mallards and Lesser Scaups. About 10 per cent of the observed ducks dropped into Swan Lake, and the others continued in a southeasterly direction.

R. A. McCabe (letter, March 18, 1958), of the University of Wisconsin, reported this duck flight as follows:

"On the morning of November 7, 1956, I hunted at Mud Lake, between Lake Waubesa and Kegnosa, 5 miles south of Madison, Wisconsin. On this particular body of water the shootable duck flight was mediocre but about 9 o'clock that morning, and for at least 1 hour, there was a phenomenal movement of birds in a northwest-southeasterly direction. I would say there were about 75 per cent divers and 25 per cent dabblers and that they were about 1,500 feet more or less, in the air."

At the Fountain Grove Wildlife Area in north-central Missouri, C. T. Shanks (letter, August 27, 1957) noted the first migrating flock at 11:00 a.m. on November 7. His account of the flight follows:

"Another group of birds came by about 10 minutes later. Both of these flocks were relatively low when I saw them, about 500 feet . . . . By the time I reached the blind at about 12:30, these low flying flocks were passing overhead about every 3 minutes. Upon reaching the blind I noticed for the first time a large migration of birds which was occurring at a much higher altitude. These high flyers were just under the clouds and were about constant, one flock directly behind the other. I estimated this flight at about 3,000 feet. They were moving out of the northwest and continuing on in a southeasterly direction.

"At about this same time flocks of gadwalls began coming in to land 100 to 150 yards out from my blind, drinking, and immediately taking to the air. According to my counts there were, on the average, 75 gadwalls landing in this area every 2 minutes. However, since they were departing so quickly there were never more than 200–300 birds on the water at any one time. It is interesting to note that they all landed exactly in the same spot. This gadwall flight continued in this manner for approximately 2 hours, which, figuring 75 every 2 minutes, calculates to 4,500 birds landing during this 2 hour period.

"During this same period, there were just as many low flying flights which passed on without stopping so that I feel it is safe to say that 9,000–10,000 gadwalls came by this particular spot between 12:30 and 2:30 p.m. This gadwall flight seemed to stop as suddenly as it started, and was replaced by an even heavier flight of mallards. The mallard flight continued for the remainder of the afternoon. By nightfall the Fountain Grove Area, which was devoid of ducks that morning, was covered with mallards."

The vanguard of the flight arrived in Tennessee, according to P. B. Smith (letter, July 19, 1957), formerly of the Tennessee Game and Fish Commission, late in the afternoon and evening of November 7. The main flight occurred all through the day of November 8, when it was reported from numerous places throughout the state.

Smith reported that he had never seen so many ducks arrive in Tennessee in so short a time. Illustrating the magnitude of the flight, he cited the two-day kill of ducks on the West Sandy hunting area: On opening day, November 7, 400 hunters averaged 0.12 ducks per man; on November 8, hunters averaged 2.1 ducks per man.

In Arkansas, the flight was first noticed at the Big Lake National Wildlife Refuge in the northeast corner of the state about 3:30 p.m. on November 7. According to D. M. Donaldson (letter, July 24, 1957) of the Arkansas Game and Fish Commission, the flight continued until dark and through most of the

following day, November 8. Upon conducting an aerial survey, Donaldson found 15,000 Mallards on the Big Lake Refuge on November 8, where only a few Mallards had occurred before. Near Weiner, Arkansas he observed the duck flight coming in from the north at altitudes from 2000 to 2500 feet. The flight was made up almost entirely of Mallards.

The vanguard of this great duck flight arrived in Louisiana at noon on November 7, 1956, according to R. K. Yancey (letter, August 5, 1957) of the Louisiana Wildlife and Fisheries Commission. The flight was detected throughout the state by a great number of observers. Yancey was in northeastern Louisiana on November 7 and observed ducks migrating at 300 to 400 feet all across that section of the state. However, he noted that the largest movements occurred along river courses. At Lake Pontchartrain in southeast Louisiana, John Newsom, Federal Aid Coordinator with the Commission, saw large numbers of ducks arrive during the afternoon of November 7.

The flight into Louisiana continued over the next two days and brought at least 1,200,000 ducks into the state, including the first major arrivals of Mallards and diving ducks. Green-winged Teals, Gadwalls, and Pintails also arrived in large numbers. As these northern ducks moved in, the bulk of the Blue-winged Teal (*Anas discors*) population which had been present departed from the state.

Iowa-Illinois Observations.—The earliest indication of a waterfowl flight in Iowa was reported by F. A. Heidelbauer (pers. comm.) of the Iowa Conservation Commission. Late in the morning of November 6, he was flying from Des Moines to Sioux City, Iowa, when two flocks of Mallards were encountered flying southeast at 1500 feet. During an afternoon aerial reconnaissance he observed a flock near Sioux City, which also was flying southeast at 1500 feet.

At 9:30 a.m. on November 7, Heidelbauer began to see migrating ducks as soon as he left the Sioux City airport. Over the Missouri River ducks were seen in an unending stream from a few hundred feet to 5000 feet above the river. Later it was learned that the flight first appeared at Onawa, Iowa, about 8:00 a.m. Migrating flocks were made up largely of Mallards, Lesser Scaups, and Redheads. The flight continued throughout the day, but by the morning of November 8 it was over.

At Spirit Lake, Iowa, Sieh first noted a few flocks of migrating Mallards at 9:00 a.m., November 7. By 9:30 a.m. the number of passing flocks had increased until ducks were constantly in view. The flight direction was to the south-southeast, and virtually all ducks passed over without stopping at local lakes.

Seth Shepard (pers. comm.) made counts of duck flocks he could see from a window of the Biology Station at Spirit Lake. In one hour, between 9:30

and 10:30 a.m., he counted 45 flocks averaging 67 ducks per flock, for a total of 3083 birds. At nearby Pleasant Lake during a 2-hour period (1:30 to 3:30 p.m.) Thomas Moen and Seth Shepard counted 90 flocks averaging 92 ducks per flock for a total of 8,311 ducks, or 4,155 per hour. The count was made of all waterfowl crossing an imaginary vertical plane, with the observers facing to the east.

At Trumbull Lake, 20 miles southeast of Spirit Lake, William Basler (pers. comm.) similarly counted 86 flocks, totaling 5,160 ducks, passing over in an hour (1:30 to 2:30 p.m.). The flight began to taper off by 3:00 p.m. in northwestern Iowa, and by 4:00 p.m. it was practically over.

Sieh obtained a "cross-section" of this flight through northern Iowa by driving east from Spirit Lake on state route No. 9 to Osage, a distance of 128 miles. The trip was made from 12:55 to 3:40 p.m. During this 2¾-hour period, 11,925 ducks in 193 flocks (4155 birds per hour) were observed crossing the highway in front of the car. The flocks were moving largely in a south-southeast direction as far east as Thompson, but farther east, between Thompson and Osage, the flight was largely to the southeast.

Table 1 shows the distribution of the waterfowl flight between Spirit Lake and Osage. The route taken across northern Iowa crossed the upper reaches of several rivers which flow to the southeast, but little relationship between the rivers of northern Iowa (Fig. 1) and the magnitude of the flight is indicated. For the most part the flight of waterfowl was passing over the fields of northern Iowa in an evenly distributed pattern. However, eastward from Lakota to Osage, the magnitude of the flight was somewhat reduced.

Accompanied by Norman White, pilot, Bellrose had been aviating up the Mississippi River Valley for five hours before sighting the first migrating duck flocks at 2:00 p.m. on November 7 near Wapello, Iowa. By 2:15 p.m., when Muscatine, Iowa, was reached, the duck flight was appreciably greater.

At Muscatine, flocks of Mallards were observed arriving at the Mississippi River from the north and northwest. Several flocks arriving from the northwest were observed to alter course 30 to 40 degrees to move southward down the bluff of the Mississippi River Valley, some 3 to 4 miles east of the river channel. A smaller number of flocks continued on a southeast course, over the fields of Illinois, apparently bound for the Illinois River Valley.

The airplane was flown northwest from Muscatine into the stream of migrating ducks. A zigzag course was pursued; each leg of the course was about 25 miles in length and centered on the Cedar River.

On the three legs of the course, each bisected by the Cedar River, counts of flocks revealed one per minute within a belt of 5 miles on each side of the river valley as opposed to one flock per two minutes farther away from the valley.

TABLE 1

NUMBERS OF DUCKS SEEN CROSSING ROUTE 9 BETWEEN SPIRIT LAKE AND OSAGE, IOWA, ON NOVEMBER 7, 1956

City	Time P.M.	Miles Travelled	Number of Ducks	Ducks per Minute	Ducks per Mile
Spirit Lake	12:55				
Superior	1:03	6	1100	138	183
Estherville	1:15	8	575	48	72
Armstrong	1:37	18	3007	137	167
Swea City	1:46	9	1310	146	146
Lakota	2:00	12	1369	86	114
Thompson	2:22	18	1690	77	94
Forest City	2:35	14	495	38	35
Hanlontown	2:54	14	1077	57	77
Manly	3:05	9	790	72	88
Osage	3:40	20	510	15	26
Total	2¾ hours	125	11,923		
Average				71	94

At Iowa City the airplane was headed south via Mt. Pleasant to Argyle, Iowa. For 11 miles, from Iowa City to Riverside, the course was adjacent and parallel to the Iowa River. In that stretch flocks of ducks were cutting across the Iowa River Valley at an angle of 40 degrees as they pursued their southeast direction of flight.

South of Riverside the magnitude of the flight began to lessen (Table 2). Also, the flight direction of the migrating birds gradually but steadily shifted from southeast at Riverside, to generally east-southeast from there to Mt. Pleasant, and to generally east from there to Argyle. Near Argyle, two flocks of ducks were observed flying southeast down the Des Moines River Valley.

At Argyle, Iowa, the airplane's course was once again altered, this time to east-southeast toward Havana, Illinois. At the Mississippi River numerous flocks of ducks were seen descending to the river, joining rapidly-forming rafts of birds which had not been present several hours earlier.

Between the Mississippi River and Havana flocks of ducks were observed at intervals flying largely either south or southeast. The magnitude of the flight was considerably less than it was in Iowa (Table 2).

The altitude of each flock of ducks was recorded on the entire aerial trip. Over the Mississippi River Channel south of Muscatine, flocks of Mallards and Ring-necked Ducks were observed at from 400 to 600 feet. Over land during mid-afternoon flocks were observed at altitudes from 2100 to 3500 feet; the bulk of the birds, however, were flying at 2400 to 2800 feet. Most of the flight was 700 to 1100 feet below the continuous cloud layer; a few

FIG. 1. Places of observation and direction of movement of two waterfowl flights, November 6–8, 1956 and October 23–25, 1957. Car and aerial transects were made of the 1956 flight in Iowa and Illinois.

flocks were observed from time to time disappearing momentarily into the base of low clouds.

As the afternoon waned, it was apparent that the flight of waterfowl descended to lower altitudes (Table 2). The last flocks, at dark, were only 500 feet above the ground.

Observations made elsewhere in Illinois aid in further delineating the November 7, 1956, duck flight. At the Spring Lake National Wildlife Refuge, near Savanna, R. V. Wade (oral comm.) noted that the flight arrived

TABLE 2

NUMBERS AND FLIGHT ALTITUDES OF DUCKS SEEN FROM AN AIRPLANE IN EAST-CENTRAL AND SOUTHEASTERN IOWA AND WEST-CENTRAL ILLINOIS ON NOVEMBER 7, 1956

City	Time P.M.	Miles Travelled	Number of Ducks	Ducks per Minute	Ducks per Mile	Average Altitude
Willow Jct.	2:45					
West Liberty	2:55	14	540	54	39	2800
Bennett	3:05	19	600	60	32	2300
Iowa City*	3:25	32	1140	57	36	2400
Riverside	3:52	11	360	51	33	2200
Ainsworth	4:00	13	300	38	23	2100
Olds	4:07	11	240	34	22	2400
Mt. Pleasant	4:15	13	180	23	14	2700
St. Paul	4:23	13	180	23	14	2300
Argyle	4:33	16	180	18	11	2000
Ferris**	4:41	13	240	30	19	1800
Colchester**	4:53	19	240	20	13	1600
Table Grove**	5:05	20	120	10	6	1100
Havana**	5:20	20	180	12	9	500
Total	2 hrs. 15 min.	214	4500			
Average				33	21	

*Landed at Iowa City airport for 20 minutes
**Cities in Illinois, others in Iowa

there about 1:30 p.m. Most of the ducks came from the northwest, but some came from the north, following the Mississippi River Valley. The bulk of the ducks continued to the southeast. It is probable that this line of flight was observed late in the afternoon of November 7, by Charles Wheat at Sterling, Illinois, about 25 miles southeast of Spring Lake. He reported (letter, June 11, 1957) that for one and one-half hours during late afternoon he saw flock after flock of Mallards passing over, heading between southeast and south-southeast, which would take these birds to the big bend of the Illinois River at Bureau, where the principal duck habitat of that famous waterfowl area begins.

The waterfowl flight was not evident on November 7 south of central Illinois. At the mouth of the Illinois River, Edward Davis (oral comm.) of the U. S. Fish and Wildlife Service did not see any migrating waterfowl until the morning of November 8, when a spectacular flight was observed. The flight continued there until early afternoon. Slightly over 100 miles farther down the Mississippi River Valley, George Arthur (oral comm.) of the Illinois Department of Conservation observed the duck flight moving down the Mississippi River Valley all day on November 8.

On the morning of November 8, White and Bellrose left the Havana, Illinois, airport at 8:00 a.m. Immediately, migrating flocks of ducks were visible

on a course 1 to 5 miles east of the Illinois River Valley. An occasional flock detached itself from the south-moving stream of birds to fly west into a strong wind. Upon reaching one of the numerous lakes or marshes the flock descended to join others already at rest on the water.

By the time the aerial observers reached Meredosia, 45 miles south-southwest of Havana, the flight stream of ducks had practically disappeared, as the bulk of the migrating birds had steadily descended to the intervening waters. Inasmuch as local observers reported a large movement of ducks into the Illinois River Valley all through November 8, it was apparent that the bulk of the birds arriving at the Illinois River during the period had temporarily ceased migrating southward.

At Meredosia the airplane was turned away from the Illinois River Valley and headed west for the Mississippi River at Quincy, Illinois. During the 45-mile flight over land, three flocks of Mallards, aggregating 280 birds, were observed flying east at altitudes of 700 to 1000 feet.

Once more White and Bellrose headed their plane up the Mississippi River Valley. A moderate flight of Mallards and diving ducks was encountered (Table 3) up to Hamilton, Illinois. From that city northward in the Mississippi River Valley, only small and scattered flocks were observed flying south. Two flocks, aggregating 130 Mallards were observed flying north, in the opposite direction to the rest of the flight.

TABLE 3

NUMBERS AND FLIGHT ALTITUDES OF DUCKS MOVING DOWN THE MISSISSIPPI RIVER VALLEY AS SEEN FROM AN AIRPLANE ON NOVEMBER 8, 1956

City	Time A.M.	Miles Travelled	Number of Ducks	Ducks per Mile	Average Altitude
Quincy	10:10				
Hamilton	10:40	35	1000	29.0	1100
Burlington	11:15	40	145	3.6	900
Muscatine	11:45	50	245	4.9	900
Rock Island	12:00	25	50	2.0	1500

GRAND PASSAGE OF 1957

Extensive Observations.—The 1957 grand passage of waterfowl began in western Saskatchewan on October 22. In an unpublished report, J. L. Nelson of the Saskatchewan Wildlife Branch and Alex Dzubin of the Canadian Wildlife Service state that at Kindersley, Saskatchewan, flocks of 25 to 300 Mallards, with some Pintails and Lesser Scaups, were observed flying southward. The migration occurred under extremely poor visibility as a result of blizzard conditions which caused the birds to fly only 100 to 200 feet above the ground.

In the western part of Saskatchewan the peak of the duck and goose exodus occurred from mid-day on October 22 to mid-day on October 23; in the eastern part of the province it occurred largely during the afternoon of October 23. An aerial survey on October 27, 28, and 29, disclosed that waterfowl north of the snow belt (north of Saskatoon, Saskatchewan) were present in their former numbers, whereas in the snow belt south of Saskatoon only a relatively few ducks were found, the bulk having departed. Freezing temperatures were common in all areas, so Nelson and Dzubin believed that snow was the factor primarily responsible for the exodus of waterfowl from southern Saskatchewan.

At Delta, Manitoba, Frank McKinney of the Delta Waterfowl Research Station reported (telegram, October 24) that there was a mass migration through the Delta Marshes on October 24, with the local ducks departing that evening, under a clearing sky.

In North Dakota at the Lower Souris National Wildlife Refuge, Merrill Hammond, refuge biologist, reported (telephone conversation, 12:00 Noon, October 24) that the mass migration began there at 7:30 a.m., October 24. The flight continued strong until 10:00 a.m. with an intensity equal to or greater than the spectacular flight on November 1, 1955. He observed a few flocks of Pintails in the flight, but the bulk of the flight was composed of Mallards. The birds passed at the rate of 2000 to 3000 per minute. The flight was headed due south at the Lower Souris Refuge.

Previous to the mass flight of ducks, Hammond reported that Gadwalls left the refuge in the evening of October 23; they left Whitewater Lake, Manitoba in the evening of October 22.

The mass flight arrived at Swan Lake, New Ulm, Minnesota, at 8:00 a.m., October 24, according to W. G. Hoerr (letter to A. H. Hochbaum, October 25, 1957). The flight continued until 2:30 p.m., and during that time Mr. Hoerr reported that everywhere one looked in the sky there were large flocks of ducks and geese, almost all of which passed over without stopping. This was the largest flight he had ever seen so early in the autumn. Although most of the duck flocks were Mallards, there was an intermingling of Pintails, Lesser Scaups, Redheads, and Canvasbacks; the geese were Canada Geese (*Branta canadensis*) and Snow Geese (*Chen hyperborea*).

On the previous day, October 23, Hoerr reported a small flight of ducks at Swan Lake, commencing about 11:30 a.m. and continuing through the day, with flocks arriving at 30- and 60-minute intervals. On October 25, the day after the mass flight, there were only a few flocks of migrating ducks, which appeared in the afternoon.

Although Lincoln, Nebraska, lies 40 miles west of the Mississippi Flyway in the Central Flyway, its proximity suggests that observations made there

reflect the waterfowl flight down the western side of the Mississippi Flyway.

George Schildman (letter, April 25, 1958) of the Nebraska Game, Forestation and Parks Commission provided some observations. After hearing geese passing over the Wildlife Building in Lincoln during the morning of October 24, Clarence Newton and he spent the afternoon observing the migration from a hilltop, 5 miles north of Lincoln. Schildman's graphic description of the flight follows:

"Strong northerly winds, and heavy overcast skies with occasional light drizzle characterized the weather. When we first arrived we started to keep a record of the strings of moving birds. In about 10 minutes we had 9 of geese and 13 of ducks. At this point by using binoculars, we could see about 10 separate bunches of birds at one time, and one which I called geese turned out to be gulls on the second look. From then on we stopped counting because of the difficulty in identifying the more distant flocks, and the rapidity in which groups of birds were moving in and out of view. It is impossible to even guess at the number of flocks we observed that afternoon. In addition to the ducks and geese, many flocks of gulls, small groups of shorebirds, and eagles and hawks passed —all going south. Several times I scanned the horizon and counted in excess of 10 flocks of moving birds.

"At 4 o'clock the flight was over. I checked my watch at 4:07 when it dawned on me that we had seen little in the last few minutes. We stayed until sundown (about 5:20) and observed only 6 or 8 flocks in the last hour and a quarter. A light streak appeared in the overcast on the western horizon about 4 o'clock.

"I went back the next morning about sunrise, and observed only one large bunch of ducks and another small group of eight. The weather had cleared during the night, and, with it, we had our first hard freeze of the year."

In southeast Missouri at the Duck Creek Wildlife Area, George Brakhage (oral comm.) of the Missouri Conservation Commission observed the start of the waterfowl flight at 9:00 a.m., October 25. The flight continued through the rest of the day, but only a few flocks were observed the following day. About 90 per cent of the southward flying flocks passed by without stopping. Some 6000 Mallards did stop at Duck Creek, and 8000 at the adjacent Mingo National Wildlife Refuge.

Seventy-five miles south of Duck Creek, David Donaldson of the Arkansas Game and Fish Commission (letter, December 16, 1957) reported that the duck flight arrived at the Big Lake National Wildlife Refuge at 11:00 a.m. on October 25. He considered it to be only a small flight of waterfowl.

A flight of 500,000 ducks arrived in Louisiana on the night of October 24 and during the day and night of October 25, according to M. M. Smith (letter, March 10, 1958) of the Louisiana Wildlife and Fisheries Commission. The flight was made up of large numbers of divers and smaller numbers of most species of dabbling ducks.

Iowa–Illinois Observations.—The earliest observation of the 1957 spectacu-

lar waterfowl flight in Iowa was made by Conservation Officer Gerald Jauron, who reported (pers. comm.) that a sizeable duck flight was starting at 12:20 p.m. on October 23 along the Missouri River north of Council Bluffs. On October 24, in the same area, he witnessed the largest day-long waterfowl migration he had ever seen. The flight continued there on October 25 but in reduced volume. The ducks came from the north, flying south down the Missouri River Valley.

At Spirit Lake, Iowa, Sieh first observed the migration at 9:10 a.m., October 24, when a flock of 50 Mallards appeared. From that time until dark, flocks of ducks passed by the Biology Station, but they were much less numerous than on November 7, 1956. An all-day count yielded 131 duck flocks and 17 goose flocks, totaling 2962 ducks and 976 geese. Ducks passed at the rate of 37.8 birds per hour, with the flight twice as large in the afternoon as in the morning. The duck flight was to the south-southeast, but the goose flight was largely to the southwest.

Twenty miles southeast of Waterloo, Iowa, along the Cedar River, P. D. Kline (letter, October 29, 1957) of the Iowa Conservation Commission made counts of migrating ducks and geese for an hour in early afternoon on October 24, and again for an hour later in the afternoon. The count from 12:45 to 1:45 p.m. amounted to 1810 ducks in 15 flocks; and from 4:09 to 5:09 p.m., 340 ducks in 8 flocks. All of the ducks were migrating in a southeasterly direction; some goose flocks were also headed southeast, but other geese were flying to the south and southwest.

In central Illinois the flight arrived at the Chautauqua National Wildlife Refuge at 1:00 p.m., October 24. From that time until 4:00 p.m., 34 flocks of Mallards, 2 flocks of Blue (*Chen caerulescens*) and Snow Geese, and 1 flock of Canada Geese were observed alighting in the lake.

At 4:45 p.m. the refuge manager, Arthur Hughlett, and Bellrose climbed the refuge's 99-foot observation tower. A census revealed that there were about 5000 newly-arrived Mallards on the lake. Other flocks of Mallards were observed swinging into the lake from the northeast, steadily increasing the size of the rafts of birds resting on the water. At first, flocks were dropping into the lake at the rate of one per minute, but as darkness approached the tempo increased and flocks of ducks were alighting at the rate of one every 10 seconds.

As great as was the number of waterfowl which stopped at Lake Chautauqua that evening, it represented only a part of the flight south. Many flocks could be seen streaming by from ½ to 2 miles east of the Illinois River Valley. A large part of this flight, however, is believed to have taken place above the almost solid overcast, for in looking south through rifts in the cloud layer, more ducks could be seen in a limited area above the clouds than below. At

one time, through a break in the overcast, four large flocks of migrating waterfowl were visible in the binocular field. Over 200 flocks containing about 25,000 ducks were observed flying past the observation tower from 4:45 to 5:30 p.m.

By dark it was estimated that 30,000 Mallards, plus several thousand Lesser Scaup, Ring-necked Ducks, and Canvasbacks had alighted on Lake Chautauqua. Two additional flocks of Blue and Snow Geese had also dropped into the lake.

On the Mississippi River at Dallas City, Illinois, Harry Canfield, a lifelong duck guide, reported (oral comm.) that the waterfowl flight arrived there late in the afternoon of October 24, continued apparently into the night, and ended at 2:00 p.m. on October 25. He considered the flight to be larger than that of November 7, 1956, but not so large as the November 2, 1955, duck flight.

Canfield noted on October 25 that several dozen flocks of ducks were flying north at extremely high altitude, at a time when the bulk of the flight was moving south down the Mississippi River Valley.

On October 25, with Norman White as pilot, Bellrose aviated down the Illinois River Valley from Havana to Grafton, Illinois, and up the Mississippi River Valley from Grafton to Rock Island, Illinois. During the aerial survey, it was noted that from Havana to Beardstown migrating waterfowl flocks (Table 4) were east of the Illinois River Valley at altitudes of 1500 to 1800 feet, with the cloud layer at 1800 to 2000 feet. Between Beardstown and Grafton waterfowl flocks were in the eastern part of the valley, but they appeared to be following it. Above Beardstown, three flocks were observed flying north against the wind at 1500 feet.

TABLE 4

NUMBERS OF DUCKS MOVING SOUTH IN THE ILLINOIS AND MISSISSIPPI RIVER VALLEYS AS SEEN FROM AN AIRPLANE ON OCTOBER 24, 1957

City	Miles Travelled	Number of Ducks	Ducks per Mile
Havana	—	—	—
Beardstown	30	600	20
Meredosia	15	180	12
Grafton	60	900	15
Clarksville	55	1200	22
Quincy	50	3000	60
Hamilton	35	1200	34
Burlington	40	800	20
Muscatine	50	600	12

TABLE 5

A 2-DAY CHANGE IN WATERFOWL POPULATIONS OF THE LOWER ILLINOIS AND MISSISSIPPI RIVER VALLEYS FROM GRAFTON, ILLINOIS, TO MUSCATINE, IOWA, IN 1956

Species	November 7	November 8	Per Cent of Change
Mallard	257,000	704,000	+63.5
Black Duck	1,500	6,400	+76.6
Gadwall	900	1,600	+43.8
Pintail	29,000	4,500	-84.5
Green-winged Teal	10,800	4,400	-59.3
American Widgeon	8,600	4,400	-48.9
Shoveler	400	400	00.0
Ring-necked Duck	4,700	83,000	+94.3
Canvasback	520	3,000	+82.7
Lesser Scaup	13,500	127,000	+89.4
Ruddy Duck	150	30	-80.0
Total	327,070	938,730	+65.2

Near St. Charles, Missouri, three flocks of geese and two flocks of ducks were observed leaving the Mississippi River where it bends to the east. The waterfowl flocks were pursued a short distance on their southward line of flight until it was ascertained that their course was to the west of St. Louis.

The intensity of the waterfowl flight in the Mississippi River Valley on October 25 (Table 4), the second day of the 1957 grand passage, was greater than it was on November 8 (Table 3), the second day of the 1956 grand passage. On the second day of the 1956 and 1957 aerial surveys, the waterfowl flight declined in magnitude above Hamilton, Illinois.

A measure of the magnitude of the massed waterfowl flights which arrived in Illinois on November 2, 1955, November 7, 1956, and October 24, 1957, is shown in Fig. 2. The figures were obtained by Bellrose from periodic aerial surveys of waterfowl populations in Illinois.

The 1955 grand passage resulted in an increase of 775,000 ducks in the Illinois River Valley; the 1956 grand passage resulted in an increase of 600,000; and the 1957 grand passage in an increase of 225,000. The species composition of the 1956 and 1957 flights is indicated by Tables 5 and 6. As in 1955, Mallards made up the bulk of the flight population, but, unlike the 1955 flight, the largest proportionate increases in local population as a result of the 1956 and 1957 massed flights occurred in Lesser Scaups, Ring-necked Ducks, and Canvasbacks.

Population figures reveal that there was a pronounced exodus of ducks from the Illinois and Mississippi River valleys concurrent with the arrival of the northern birds. In 1956, the principal species departing were the Pin-

TABLE 6

WATERFOWL POPULATION CHANGES ON LAKES IN THE ILLINOIS RIVER VALLEY FROM PEKIN TO HAVANA, ILLINOIS, ON THREE DAYS IN 1957

Species	October 22	October 24	October 25	Per Cent of Change
Mallard	6,900	19,100	111,500	+ 82.9
Black Duck	380	655	675	+ 3.0
Gadwall	45	85	1,100	+ 92.3
Pintail	500	1,500	500	- 66.6
Green-winged Teal	1,800	1,250	650	- 48.0
American Widgeon	3,650	1,010	2,800	+ 63.1
Shoveler	70	60	50	- 16.7
Ring-necked Duck	0	0	10,000	+100.0
Canvasback	0	0	500	+100.0
Lesser Scaup	0	0	6,500	+100.0
Total	13,345	23,660	134,275	+ 82.4

tail, Green-winged Teal and American Widgeon (*Mareca americana*) (Table 5). In 1957, the Pintail and Green-winged Teal departed in large numbers (Table 6).

MECHANICS OF MIGRATION

The piecing together of visual records of the directions taken by migrating waterfowl supplement information on flyway routes provided by band-recovery data. Band recoveries do not fix as finitely as visual records, specific routes of passage in any geographic area.

An analysis of the flight directions reported for November 1–3, 1955 (Bellrose, 1957:20), and those of November 6–8, 1956, and October 23–25, 1957 (Fig. 1), adds materially to the available knowledge on routes taken by waterfowl in the Mississippi Flyway.

From the plains of Saskatchewan and Manitoba to Illinois the general direction of flight was between south-southeast and southeast. In the area between northern (latitude 42°30') and south central Illinois (latitude 39°), there was a great wheeling movement as the bulk of the flight turned from a southeasterly direction to a southerly one. It appeared as if the Mississippi River played a major role in changing the course of the migrants, with the Illinois River playing a secondary role and other bodies of water, such as the Chain-of-Lakes in northeastern Illinois, tertiary roles. In other states, significant bodies of water might serve in a similar fashion.

The key role that certain water areas may serve in altering direction of flight was illustrated by the fact that duck flocks changed their course from

southeast to south when they arrived at the Mississippi River near Muscatine, Iowa. Although other duck flocks continued in flight to the southeast, observations made of the November 2, 1957, flight and other flights indicated that they changed to a more southerly direction at the Illinois River. On the basis of observation on past flights, such migrating flocks as those observed by McCabe in Wisconsin are thought to have shifted to a southerly direction in the Chain-of-Lakes region in northeastern Illinois.

There was a strong flight of waterfowl down and adjacent to the Missouri River Valley in Iowa. Because the bulk of the movement did not turn east at Kansas City, Missouri, to follow the Missouri River, the plausible conclusion was that the flight continued in a south-southeasterly direction over the Ozark Mountains to wintering grounds in Arkansas and Louisiana.

Sieh did not observe any tendency for migrating waterfowl to follow rivers when he crossed northern Iowa on November 7, 1956. Duck flocks were dispersed all across the northern part of the state (Table 1). Farther down the flight lines, where the streams were larger, Bellrose's observations indicated that migrating waterfowl were more abundant within 5 miles of the Iowa and Cedar Rivers, which flow from northwest to southeast; however, he found ducks migrating across all of southeastern Iowa (Table 2). It appeared that as the rivers became larger, there was a tendency for the ducks to use them as guide lines, but only when river courses paralleled the lines of flight. Migrating waterfowl appeared to depart from river guide lines whenever they were inconvenient to follow, as exemplified by flocks leaving the Mississippi River above St. Louis to fly straight south.

The migrating flocks observed flying southward between the Mississippi and Illinois rivers (Fig. 1) may well have turned south at some point on the Mississippi River directly north of the place where they were observed. At three different latitudes duck flocks were observed heading directly east from the Mississippi River toward the Illinois River; again these birds may have used some point on the Mississippi to alter their line of flight.

Flocks observed flying north at the same altitude as the stream of southbound migrants are thought to be ducks which arrived at the Mississippi River at a point south of the desired one. These ducks would appear to have recognized their displacement from land marks, and used them as a means of returning to their haunts of other years.

In aviating inland from the Mississippi River between Iowa City and Argyle, Iowa, on November 7, 1956, it was obvious that the direction of duck flight changed from southeast to east by the time Mt. Pleasant was reached. Apparently most flocks headed directly toward the Mississippi River as darkness approached. From an altitude of 2500 feet the river was barely

discernible 20 to 30 miles away, and apparently as the birds saw it, they swung east toward it. Most ducks appeared to be halting their flight for part or all of the night when they reached the river.

The waterfowl passage on November 7, 1956, was on a front of at least 250 miles. The first migrants formed a line which at 9:00 a.m. was farthest south near Omaha, Nebraska, and slanted abruptly to the north-northeast, extending at least as far as Minneapolis, Minnesota. The location of the front line of migrants is derived from observations of the first ducks which appeared in the Missouri River Valley at Onawa, Iowa, at 8:00 a.m., at Spirit Lake, Iowa, at 9:00 a.m.; at Swan Lake near New Ulm, Minnesota, at 9:00 a.m.; and at Minneapolis, Minnesota, at 9:00 a.m. (Fig. 1). Thus the western terminus of the flight line in the Mississippi Flyway was about 200 miles south of the eastern segment of the flight line at Minneapolis.

The apparently greater progress southward in the west segment of the flight over the segments farther east no doubt stems from the fact that these mass waterfowl migrations often start from the western plains of Canada ahead of those from the eastern plains. This was recorded on the October 31–November 3, 1955, flight (Bellrose, 1957:19), and on the October 22–25, 1957, flight. In 1957, the passage peaked between the noons of October 22–23 in western Saskatchewan, and during the afternoons of October 23 in eastern Saskatchewan and October 24 farther east at Delta, Manitoba.

Counts made in Iowa at Spirit Lake, across northern Iowa from Spirit Lake to Osage (Table 1), and in eastern Iowa (Table 2) on November 7, 1956, indicate that that flight was much greater in the western part than in the eastern part of the Mississippi Flyway. Even though observations were made from fixed points, from a car, and from a plane the results were roughly comparable because all counts were made at an approximate right angle to the line of flight. Thus a moving observer would not tend to expand or compress the magnitude of the flight as long as observations formed a cross-section; his zone of observation would remain of comparable size.

Rate of Movement.—During the 1956 grand passage certain observers were in a position to notice the first major wave of migrating ducks reaching their locality. They also reported the flight directions which made it possible to project probable lines of flight.

A comparison of the arrival of ducks at selected points, 250 to 270 miles apart and along projected lines of flight, makes it possible to roughly compute the speed of the 1956 mass migration through the Midwest.

Ducks observed passing over Swan Lake near New Ulm, Minnesota, at 9:00 a.m., on November 7, and moving in the direction of Muscatine, Iowa, were probably representative of the birds which reached that area at 2:15 p.m. It is about 260 miles from Swan Lake to Muscatine, and the ducks appeared

to cover this distance in 5¼ hours for an average flight speed of 50 mph. The flight which passed Minneapolis, Minnesota, probably represented the same section of the migration which reached Savanna, Illinois, 5½ hours later and some 250 miles to the southeast for a speed of 45 mph. The Mallards that reached Sumner, Missouri, at 2:30 p.m. were probably in the section of flight which passed Spirit Lake, Iowa, at 9:00 a.m. These ducks probably travelled 270 miles in 5½ hours, for a speed of 49 mph.

Amazing though it seems, it is probable that ducks which left central Saskatchewan during the day on October 23, were the ones which arrived in Louisiana the night of October 24. This indicates a continuous flight for about 36 hours covering some 1500 miles (±200 miles) for an average speed of 40 mph.

Both the 1956 and 1957 grand passages of waterfowl arrived in Louisiana at almost the same time as in Illinois, even though central Louisiana is some 600 miles south of central Illinois. The fact that ducks did not appear in eastern Arkansas until the following day, strongly suggests that the early arrivals in Louisiana flew 150–200 miles west of the Mississippi River, on a south-southeast course. Probably these flights crossed western Iowa during the afternoon and night. The flocks Heidelbauer observed in migration on the afternoon of November 6, 1956, in western Iowa probably represented this pulse of the flight. Apparently Jauron saw the start of this segment of the 1957 flight at 12:20 p.m. on October 23, when it began to pass down the Missouri River Valley near Onawa, Iowa. The segment of the grand passage observed at Bismarck, North Dakota, and Fergus Falls, Minnesota, on the morning of November 6, 1956, may represent part of this passage which reached Louisiana on November 8.

Altitude.—Under high overcast skies on November 7, 1956, ducks were found migrating from 2100 to 2800 feet over the farm lands of Iowa (Table 2). As darkness approached, the ducks dropped lower and lower until at dark they were only 500 feet above the ground. A similar decline in altitude with the waning of the day was also observed near Minneapolis, Minnesota. There Donald Smith estimated that flocks of waterfowl descended from 2000 feet in mid-day to 800–1000 feet late in the afternoon.

On November 8, 1956, migrating flocks were found from 900 to 1500 feet above the Mississippi River (Table 3), and in the same area on October 24, 1957, they were found at altitudes varying from 1100 to 1700 feet. Over Arkansas, they were recorded at 2000 to 2500 feet. In western Iowa, several flocks were recorded at 1500 feet on November 6, 1956.

Weather Conditions.—Weather conditions associated with the November 6–7, 1956, waterfowl flight from the northern Great Plains region were under the influence of a moderate low which, on November 5, moved north-north-

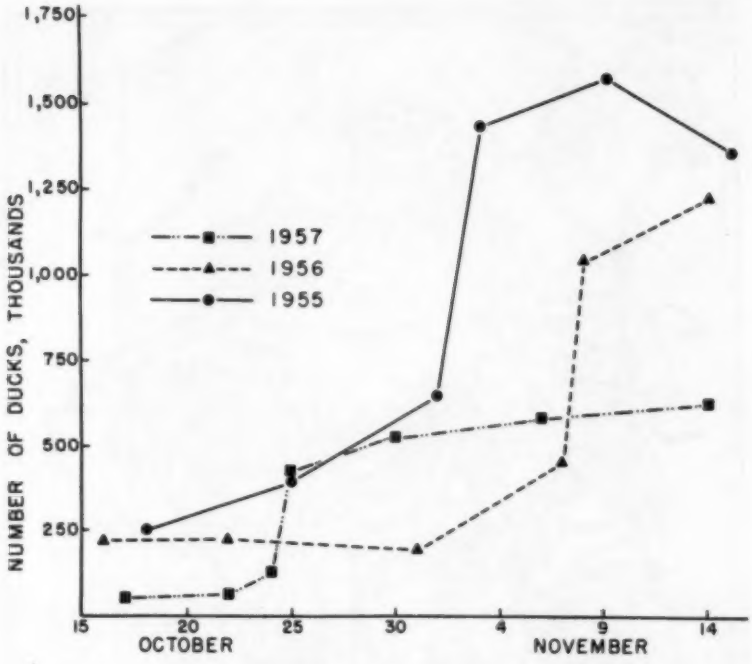

FIG. 2. Changes in the waterfowl population of the Illinois River Valley resulting from a mass migration in each of the three years, 1955–1957.

west from western Iowa to center in southwestern Manitoba by 12:30 a.m. on November 6.

Apparently as the low pressure area passed through North Dakota, it, or the weather associated with it (Fig. 3), induced some movement of ducks out of that state, beginning late in the afternoon of November 5. By the morning of November 6, much larger numbers of ducks were reported moving through central North Dakota, western Minnesota, and southern Manitoba.

The weather map for 12:30 a.m. (C.S.T.) on November 7 (Fig. 4) shows that the low pressure area had deepened slightly and had become extended to form a trough from southeastern Ontario to James Bay. Weather associated with this low consisted of falling temperature; overcast skies through eastern Ontario, Manitoba, eastern Saskatchewan, and south through Minnesota, North and South Dakota; falling snow in a belt from eastern Ontario, through

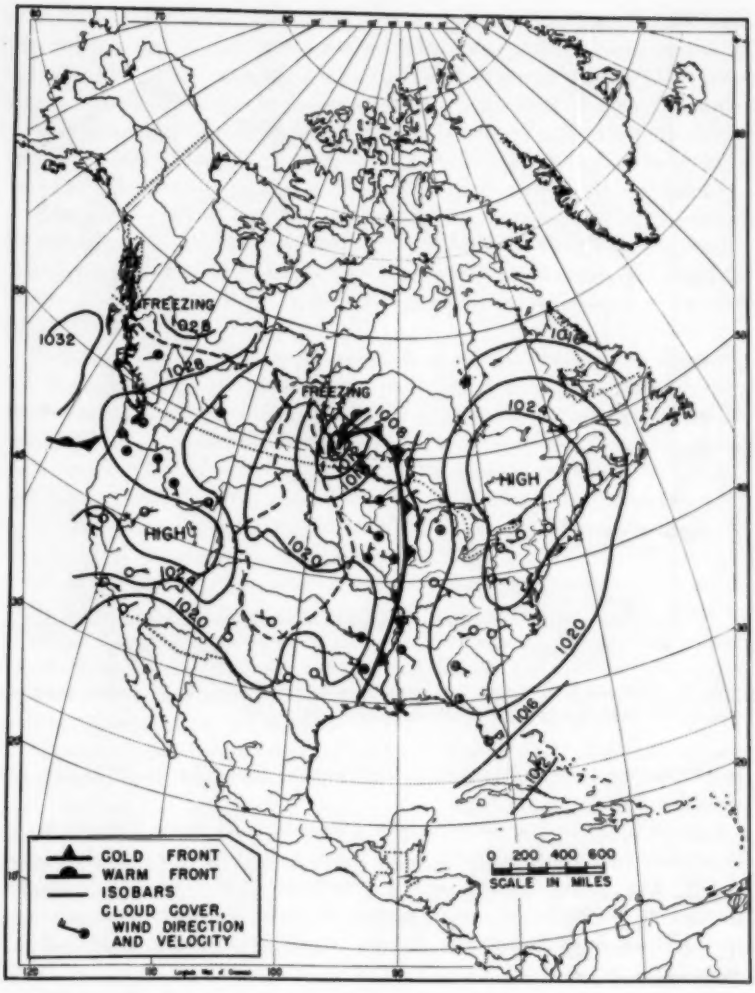

FIG. 3. Weather conditions as of 1:00 a.m. (C.S.T.), November 6, 1956, according to the United States Weather Bureau.

southern Manitoba to central Saskatchewan; and winds from the northwest in the northern Great Plains region.

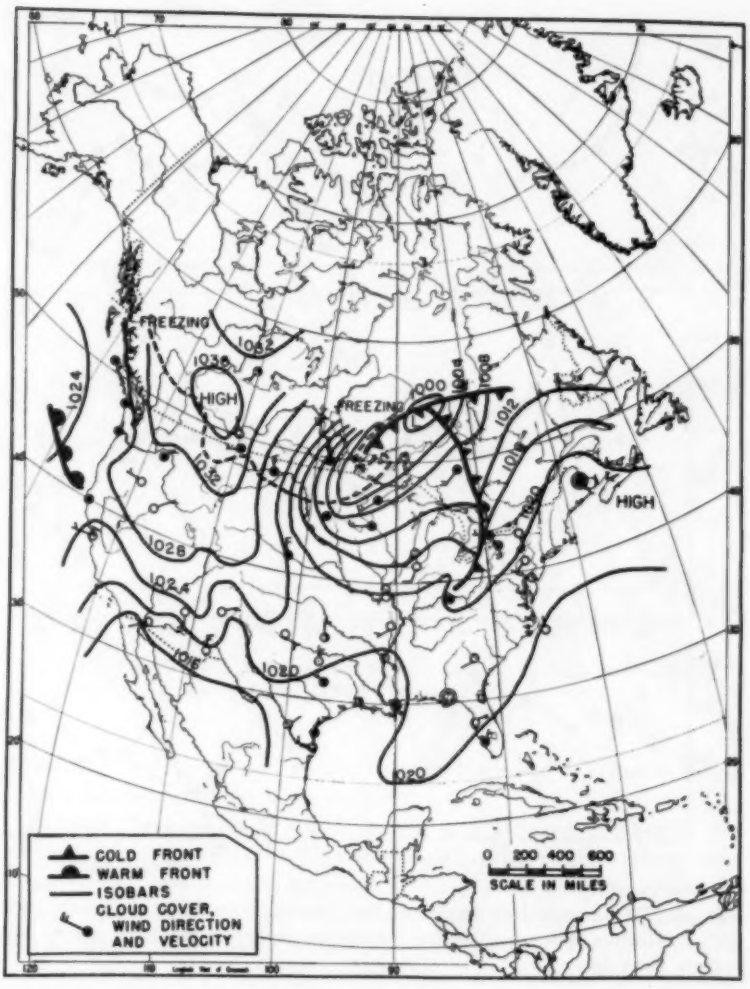

FIG. 4. Weather conditions as of 1:00 a.m. (C.S.T.), November 7, 1956, according to the United States Weather Bureau.

Daily weather records at Winnipeg, Manitoba, show (Fig. 5) that on November 5, 1956, the minimum temperature rose slightly but fell 6 degrees

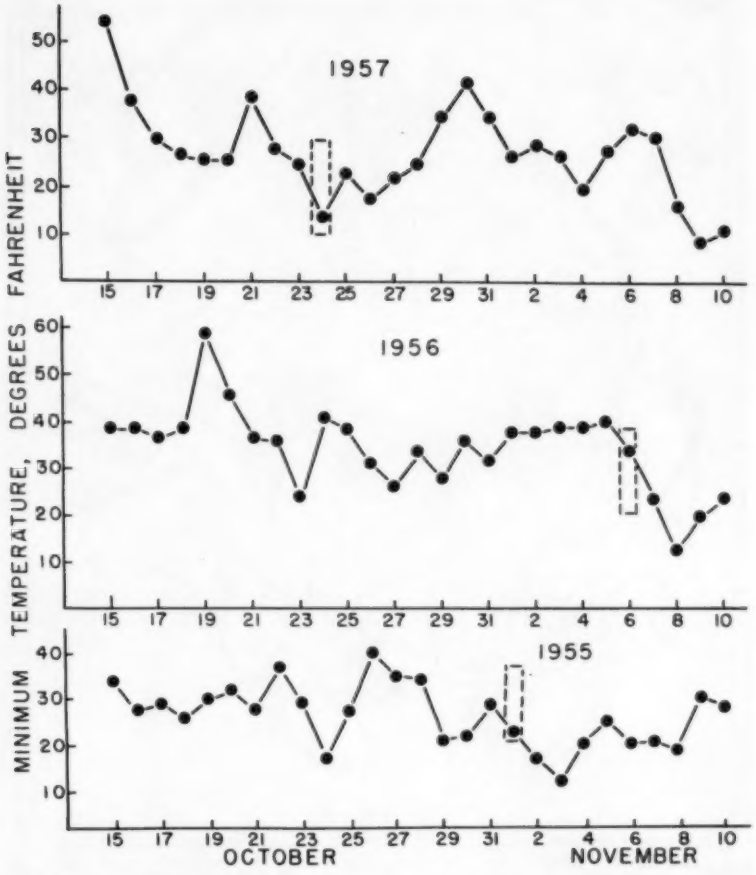

FIG. 5. The minimum daily temperature from October 15 through November 10, 1955–1957, at Winnipeg, Manitoba, Canada. Vertical bar designates day flight started from southern Manitoba.

on November 6, 8 degrees on November 7, and 11 degrees on November 8, when a low temperature of 13 degrees was reached. Daily weather records of Saskatoon, Saskatchewan, 450 miles northwest of Winnipeg, show (Fig. 6) that temperatures as low as 4 degrees above zero occurred there as early as October 29, followed by a slight warming trend on October 31, near zero on

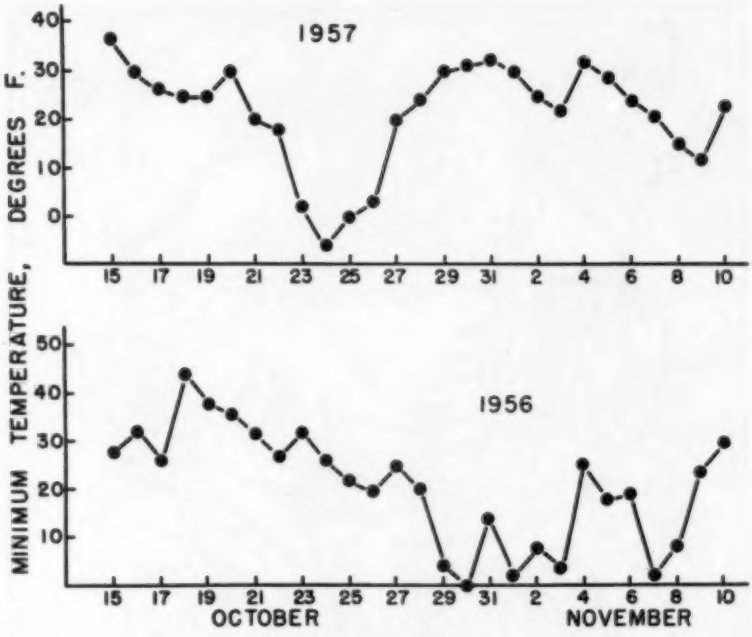

FIG. 6. The minimum daily temperatures from October 15 through November 10, 1956 and 1957, at Saskatoon, Saskatchewan, Canada.

November 1 and 2, a strong warming trend on November 4, 5, and 6, followed by a return of cold air on November 7.

Moderate flights of ducks which arrived in Illinois on October 31 and November 3 (not indicated by population data because of departure of other ducks, Fig. 2) were probably triggered by the cold air which penetrated the Saskatoon, Saskatchewan, area on October 29 and November 1. Because this cold air did not extend as far southeast as Winnipeg (Fig. 5), the bulk of the ducks which may have departed from the Saskatoon area at that time probably halted their migration north of the border.

They were then in position to become affected by the weather (produced by the low pressure area moving north from Iowa) which brought storm conditions to southern Manitoba and Saskatchewan on November 6 and 7. As indicated by temperature and wind changes at Winnipeg (Table 7), the flight probably started from this region about midnight on November 6, when

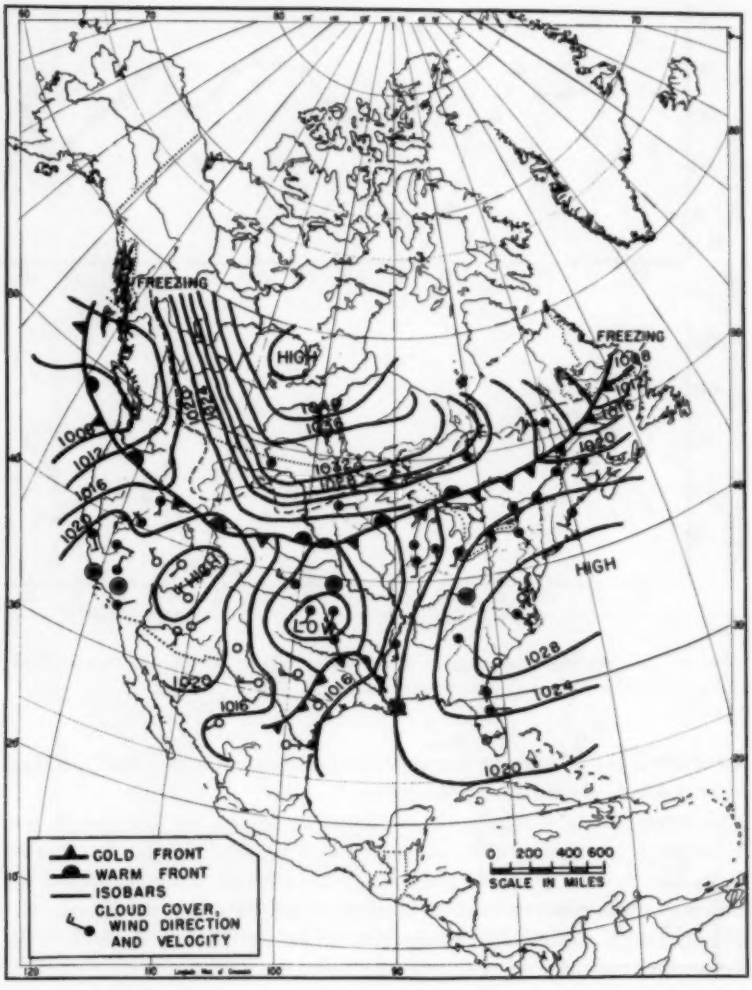

FIG. 7. Weather conditions as of 1:00 a.m. (C.S.T.), October 23, 1957, according to the United States Weather Bureau.

the wind shifted from north to northwest and increased in velocity. Temperatures fell slowly but steadily, reaching a low of 13 degrees at Winnipeg on November 7.

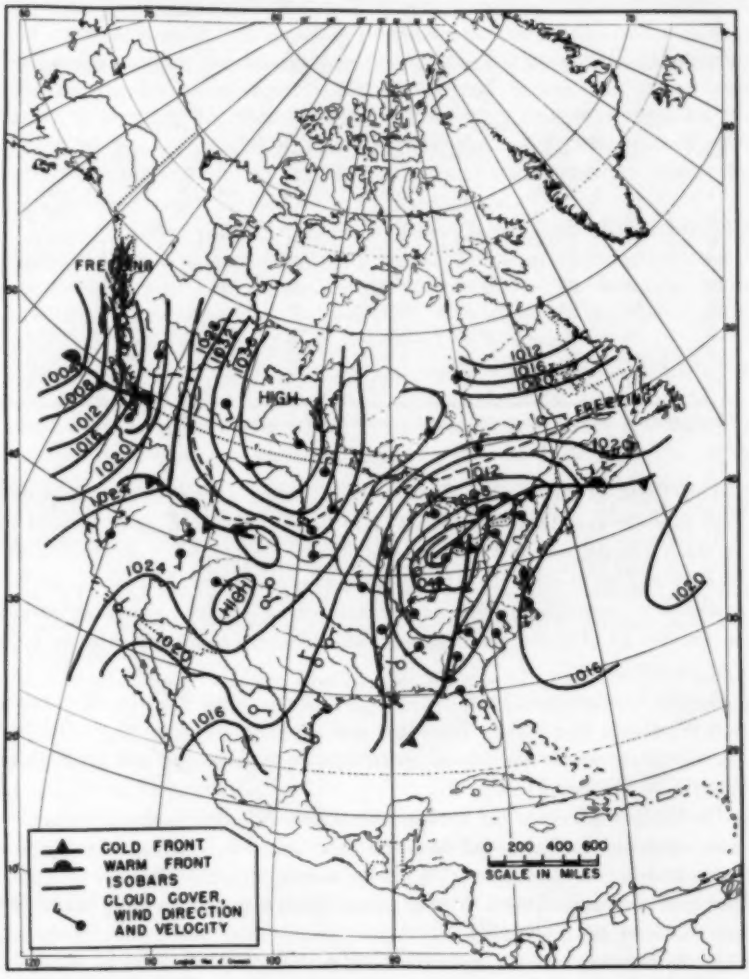

FIG. 8. Weather conditions as of 1:00 a.m. (C.S.T.), October 24, 1957, according to the United States Weather Bureau.

The 1957 grand passage started in western Saskatchewan about mid-day on October 22, in eastern Saskatchewan during the afternoon of October 23, and in Manitoba probably about midnight, October 23.

TABLE 7

WEATHER CONDITIONS[1] AT WINNIPEG, MANITOBA, NOVEMBER 6–7, 1956, AND OCTOBER 23–24, 1957

Hour of Day	1956 November 6 Temp.	Wind	1956 November 7 Temp.	Wind	1957 October 23 Temp.	Wind	1957 October 24 Temp.	Wind
1	38	S 26	31	NW27	28	NE18	25	NW17
3	37	S 25	28	NW25	27	NE17	26	NW 8
6	37	S 20	25	NW27	26	NE16	25	NW14
9	36	S 19	25	NW26	27	NE15	29	NW20
12	36	S 9	26	NW27	31	NE19	32	NW21
15	36	SW 7	27	NW25	27	NE19	36	NW19
18	36	N 8	26	NW24	26	NE17	30	NW14
21	35	N 16	25	NW13	27	NE16	26	NW14
24	33	NW24	17	W10	25	NE17	24	NW16

[1]Temperature in degrees Fahrenheit; wind direction; and velocity in mph.

This flight of ducks from Canada started when a very large and strong high pressure area moved southeast from the Yukon Territory of Canada to northern Alberta, where it was centered at 6:00 a.m. (C.S.T.) on October 22. By 6:00 a.m. on October 23 (Fig. 7) the high pressure area had moved farther southeast to central Saskatchewan, and from there it moved slowly southward on October 24 (Fig. 8), reaching the United States–Canadian border by 6:00 a.m. on October 25.

A cold front moving south through Wyoming, South Dakota, Minnesota, and Wisconsin on October 22 stalled and partially disappeared on October 23, when a moderate low moved northeastward to Missouri, and on to Lake Ontario by October 24 (Fig. 8).

On October 22, snow fell most of the day in Alberta, southern Saskatchewan, southern Manitoba, and Montana; and rain fell in the northern plains states and in the Midwest. The entire northern Great Plains was under obscured or overcast skies. In that region winds were largely from the northeast and east at 15–25 mph.

Snow continued to fall through the morning of October 23 in southern Alberta, southern Saskatchewan, the southwest corner of Manitoba, and northern Montana. Snow showers occurred in North Dakota and rain fell through much of the Midwest. Skies were obscured or overcast through most of the northern Great Plains and the Midwest. In the Great Plains and north-central United States winds were mainly from the northeast at 15–25 mph, shifting to the north as the day progressed.

During the morning of October 24, snow continued to fall in North Dakota and scattered snow storms occurred in Minnesota and South Dakota. Skies became clear in the prairie provinces, and as the day progressed the clearing extended southward through North Dakota and Minnesota. Skies were largely overcast in the Midwest during the morning, and the overcasting increased as the day progressed. In Manitoba and Saskatchewan winds were largely westerly early in the day, shifting to northwest later in the day as the high pressure moved farther south in Saskatchewan.

The high pressure area, with its clockwise flow of air, began bringing continental arctic air into Alberta on October 21. This cold air mass moved into Saskatchewan and northern Montana on October 22, and into North Dakota during the afternoon of October 23. On October 24, the cold air mass moved to South Dakota and thence eastward to Wisconsin.

This cold air mass produced a similar sequence in temperature decline at both Saskatoon, Saskatchewan, and Winnipeg, Manitoba (Figs. 5 and 6). However, as might be expected, the temperature decline during the period of October 21–24 was more severe at Saskatoon than at Winnipeg. The –6°F. reported at Saskatoon was an unusually low temperature for the season.

Calculating the time of the waterfowl flight on October 24 from its apperance in the Midwest suggests that ducks may have started migrating from southern Manitoba about 1:00 a.m. on that date. About that time the wind shifted from northeast to northwest (Table 7). The temperature which had dropped 6 degrees since noon, remained at or near 25°F. through the early morning hours.

Effect of Weather on Mass Flights.—An analysis of weather conditions occurring at the time of the massed waterfowl flights on October 31–November 3, 1955 (Bellrose, 1957:21–24), November 6–8, 1956, and October 23–25, 1957, points to several similar and dissimilar weather conditions in association with the three flights.

Barometric Pressure.—Two massed waterfowl flights (1955 and 1956) occurred as a result of weather conditions associated with low pressure areas, and one massed flight (1957) was initiated by weather conditions produced by a high pressure area. It is difficult to assess the role of barometric pressure alone as a factor in triggering waterfowl flights. The low center passing through North Dakota on November 5, 1956, may have resulted in some ducks migrating in advance of storm conditions. Certainly, the peaks of the 1955 and 1956 massed flights were more directly associated with weather conditions than with low pressure, and the 1957 flight was definitely not the result of low pressure.

Atmospheric Conditions.—The massed flights in all three years were associated with overcast skies which prevailed over almost the entire north-

ern Great Plains and south through the Midwest. In the Midwest we observed massed flights in the daytime only under overcast skies.

For example, November 7, 1956, began as a clear day in Illinois. By 1:30 p.m., a solid overcast moved in from the northwest along the Mississippi River.

At 2:30 p.m., the front line of migrating ducks appeared, as previously described, at Muscatine, Iowa. Both the duck flight and overcast skies persisted until darkness. On other occasions we have observed duck flights to end shortly before or after the overcast passed regardless of the time of day.

All three flights originated when snow was falling extensively on the plains of Canada. Usually the snow had been falling for several hours, or longer, before the first migrating waterfowl were observed. The importance of snow as a factor in large scale waterfowl migrations is apparent in Nelson's and Dzubin's October, 1957, observations of the almost complete exodus of ducks from the snow belt south of Saskatoon, Saskatchewan, as opposed to ducks remaining in customary numbers north of there.

Observations made on the Pink-footed Goose (*Anser brachyrhynchus*) in central Iceland by Jones and Gillmor (1955:163) led them to conclude that snow was the most important factor in their fall departure. They stated:

"The two departures in the two snows were forced departures. . . . The geese which left in the second snow were actually leaving on their migration to Britain. Some arrived the same day as they left, others the next day. . . . Temperature alone seems to have very little effect on geese."

Wind.—In the three massed duck flights studied, the wind was never unfavorable on the northern Great Plains when the migrations started. At the time of the November 1, 1955, flight winds were largely westerly through southern Manitoba and North Dakota (Bellrose, 1957: 15, 22); they were more northerly to the north and west of there. Although farther south in the Mississippi Flyway wind direction was flanking or adverse, winds in Manitoba and Saskatchewan, where a large part of the migration originated, were partially to fully favorable.

Early migrants on the November 6–8, 1956, movement experienced flanking winds for the most part. However, winds became exceedingly favorable by November 7, and it seems evident that the bulk of the flight developed with the shift in wind to the northwest (Table 7), which would provide a tail wind.

Again on the October 22–24, 1957, mass movement from the plains, winds were flanking in the early stages of the migration, but the winds shifted more and more to a favorable northwest direction as the day of October 24 progres-

sed. The bulk of the flight appears to have developed from Manitoba about the time the wind shifted from northeast to northwest (Table 7).

Wind apparently was a factor in reducing the magnitude of a waterfowl flight on October 24, 1955. About equally low temperatures prevailed on that same day in 1955 and 1957 (Fig. 3). Although there was a flight from the northern plains on October 24, 1955, it was much below the proportions of the one on October 24, 1957. One difference in the weather conditions was the wind, which on October 24, 1955, at Winnipeg, Manitoba, was light and from the west, southwest and south.

Temperature.—All three of the waterfowl flights under discussion occurred when temperatures were in the process of dropping to lows of 17° on November 2, 1955; 17° on November 7, 1956; and 24° on October 24, 1957, at Winnipeg, Manitoba (Fig. 5 and Table 7). Data recorded on weather maps indicate that temperatures on the southern plains of Saskatchewan dropped to similar minimums 12 to 24 hours ahead of Winnipeg on the occasion of all three duck flights. In 1956, temperatures dropped to seasonal lows at Saskatoon, Saskatchewan, several days ahead of the change at Winnipeg, but in the 1957 period temperature changes were similar in chronology at both cities.

Analysis of Weather Factors and Mass Migration.—Three spectacular waterfowl flights in as many years resulted from storm conditions on the northern Great Plains. The elements responsible for the storms were created by low pressure areas in two years and a high pressure area in one year.

The weather elements which appeared to contribute to these massed flights were: extensive overcast skies, falling snow, fairly strong winds which were partially or entirely favorable in the areas where the flights originated, and falling temperatures which in southern Manitoba declined at least to the low 20's. A cold front was involved in the 1955 massed flight, but not in those of 1956 and 1957.

Summary

1. Spectacular waterfowl flights, sometimes referred to as "grand passages," occurred in the Mississippi Flyway on October 31–November 3, 1955; November 6–8, 1956; and October 23–25, 1957.
2. The massed waterfowl flight of 1955 was discussed in detail in an earlier paper; the present paper discusses the flights of 1956 and 1957, with particular emphasis on their passages through Iowa and Illinois.
3. Observers at numerous places from southern Manitoba to Louisiana reported the movements of waterfowl. The 1956 massed flight was first noted passing through southern Manitoba and in the vicinity of Bismarck, North Dakota, and Fergus Falls, Minnesota, during the morning of November 6.
4. The "leading edge" of one pulse of the flight reached Onawa, Iowa, on the Missouri River at 8:00 a.m., November 7, 1956, and Spirit Lake, Iowa, New Ulm and Minneapolis, Minnesota, at 9:00 a.m. Migrant flocks continued en masse

over these points until the flight slackened appreciably at each location about 3:30 p.m.

5. Counts of flocks migrating in the region of Spirit Lake, Iowa, indicated a passage of 3083 ducks per hour from 9:30 to 10:30 a.m., and 4155 ducks per hour from 1:30 to 3:30 p.m.
6. A "cross section" of the waterfowl passage on November 7, 1956, through northern Iowa was obtained by driving eastward from Spirit Lake to Osage, a distance of 128 miles. Ducks crossed this line of observation at the rate of 4260 birds per hour from 12:55–3:40 p.m.
7. A cross section of the waterfowl passage through east-central Iowa was obtained from a light airplane. At the Mississippi River near Muscatine, Iowa, the "leading edge" of the flight appeared at 2:15 p.m., November 7, 1956. The waterfowl flight was observed as the plane took a zigzag course to Iowa City and thence south parallel to the Mississippi River to Argyle, Iowa, and eastward to Havana, Illinois. Ducks crossed the line of flight in Iowa at the rate of 2520 ducks per hour, and in Illinois at the rate of 996 ducks per hour.
8. The vanguard of this massed flight arrived in Louisiana at noon on November 7, 1956, and continued for two days, bringing at least 1,200,000 ducks into that state.
9. The 1957 grand passage of waterfowl began in western Saskatchewan on October 22, where it peaked that afternoon and the following morning; in eastern Saskatchewan the flight occurred largely during the afternoon of October 23; and at Delta, Manitoba, it took place largely on October 24.
10. In North Dakota at the Lower Souris National Wildlife Refuge mass migration commenced at 7:30 a.m. on October 24, 1957, and continued strong until 10:00 a.m. It appeared at Swan Lake, Minnesota, at 8:00 a.m. and continued there to 2:30 p.m.
11. A segment of the grand passage appeared on the Missouri River in western Iowa at 12:20 p.m. on October 23, 1957. However, farther east in Iowa the flight did not appear until October 24, reaching Spirit Lake at 9:10 a.m. It continued through the day, but the rate of flight was only 378 ducks per hour, about one-sixth of the magnitude of the 1956 flight.
12. Although a few migrating ducks appeared in central Illinois at 1:00 p.m., October 24, 1957, the main body of migrants arrived at 4:45 p.m. and continued into the night. During the period it was estimated that 25,000 ducks passed the Chatauqua National Wildlife Refuge and a slightly larger number dropped into the lake.
13. The 1955 grand passage of waterfowl resulted in an increase of 775,000 ducks in the Illinois River Valley; the 1956 grand passage resulted in an increase of 600,000 ducks; and the 1957 massed flight in an increase of 225,000 ducks in that area.
14. A half-million ducks were estimated to have arrived in Louisiana on the night of October 24, and the day and night of October 25, 1957.
15. Flight directions recorded during the spectacular flights of 1955, 1956, and 1957 were generally between south-southeast and southeast from the plains of Saskatchewan and Manitoba to Illinois. Certain water areas may serve a key role in altering direction of flight as indicated by flocks shifting from southeast to south when they arrived at the Mississippi River Valley.
16. The waterfowl passage on November 7, 1956, was on a front more than 250 miles in length, extending from near Omaha, Nebraska, north-northeastwardly to Minneapolis, Minnesota, and probably in both directions beyond those points.

17. The mass migration of October 31–November 3, 1955, and October 23–October 25, 1957, progressed southward in the west ahead of the east in the Mississippi Flyway probably because migrations started from the western plains of Canada ahead of those from the eastern plains corresponding with weather impetus. Counts on November 7, 1956, indicate that the flight was much greater in the western segment than in the eastern segment of the Mississippi Flyway.
18. A series of observations during the grand passage of 1956 indicate a ground speed from 45–50 mph. Ducks leaving central Saskatchewan on the day of October 23, 1957, suggest a continuous flight to Louisiana, a distance of 1500 (±200) miles for an average speed of 40 mph.
19. Arrivals in 1956 reached Illinois and Louisiana within a few hours of each other, strongly suggesting that the early arrivals in Louisiana flew 150–200 miles west of the Mississippi River, and were ahead of flight segments migrating farther east before they turned south.
20. The altitude of migrating ducks over the fields of Iowa and Illinois varied from 1500 to 2800 feet during the day. As darkness approached, flocks of ducks dropped lower to a minimum of 500 feet.
21. The weather responsible for the three massed duck flights was created by low pressure areas in two years and a high pressure area in one year. The weather elements associated with the flights were: extensive overcast skies, falling snow, fairly strong winds which were partially or entirely favorable in areas where the flights originated, and falling temperatures which in southern Manitoba declined to the low 20's.

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SOME ANATOMICAL CHARACTERS OF THE CUCULIDAE AND THE MUSOPHAGIDAE

BY ANDREW J. BERGER[1]

MOST authors have placed the African touracos ("plantain-eaters") and the cosmopolitan cuckoos in a single order, the Cuculiformes or Cuculi (e.g., Mayr and Amadon, 1951, Wetmore, 1951). Bannerman (1933), Moreau (1938, 1958), Lowe (1943), and Verheyen (1956*a*, 1956*b*), however, believed that the touracos deserve ordinal rank, the Musophagiformes. I agree with these authors but not for some of the reasons they cite.

I have been interested in the anatomy and relationships of these two groups of birds for over a decade, but it now seems unlikely that it will be feasible to continue this work. Consequently, I have decided to publish certain information which, although still very incomplete, may prove useful to other investigators. The complete appendicular myology of a touraco apparently has never been described. My plan, therefore, is to describe this musculature for *Tauraco leucotis donaldsoni* ("*Turacus donaldsoni*") and then to compare the myology, osteology, and pterylosis of this touraco with that of the cuckoos. Such a comparison can not be made properly without also analyzing differences in morphology within the family Cuculidae.

This paper is based on the dissection of one or more specimens of the following genera and species of cuckoos: *Carpococcyx radiceus, Centropus bengalensis, C. superciliosus, Ceuthmochares aereus, Chrysococcyx cupreus, Ch.* ("*Lampromorpha*") *klaas* and *caprius, Ch.* ("*Chalcites*") *basalis, Clamator jacobinus, Coccyzus americanus, C. erythropthalmus, Coua serriana, C. reynaudii, C. ruficeps, C. cristata, C. caerulea, Crotophaga sulcirostris, Cuculus canorus* and sp., *Dromococcyx pavoninus, Geococcyx californianus, Guira guira, Morococcyx erythropygus, Piaya cayana, Phaenicophaeus pyrrhocephalus, Saurothera merlini, Surniculus lugubris, Tapera naevia.* These 18 genera represent less than half of the 38 genera recognized by Peters (1940), although several of his genera have been suppressed by later workers (e.g., Mayr, 1944; Delacour and Mayr, 1945; Delacour, 1946; Berger, 1955*b*). Consequently, it must be borne in mind that conclusions and generalizations presented here may have to be altered when data become available on the remaining genera of cuckoos. As a matter of convenience for other workers, I have, by and large, used Peters' genera and species of cuckoos. I do this in part because I do not agree with those who propose that it is not necessary to examine the internal anatomy of a given species merely because an earlier genus has been suppressed and its contained species have been placed in some other genus. Evidence presented here certainly casts doubt on the wisdom of

[1] I dedicate this paper to Erwin Stresemann on the occasion of his 70th birthday.

synonymizing some genera of cuckoos, as has been done on the basis of external characters alone.

Over the years I have received alcoholic specimens from several generous cooperators: Dean Amadon, Jacques Berlioz, Ernest P. Edwards, Herbert Friedmann, Mrs. Richard R. Graber, Theodore Miller, Renaud Paulian, Helmut Sick, George M. Sutton, P. B. Uzzell, and John G. Williams.

Some of the material from museums had been collected many years ago. In a few specimens, an incision through skin and muscle had been made from chin to vent. It is difficult (and sometimes impossible) to determine accurately the details of the ventral feather tracts in such birds. In two specimens, the articulations of the sternal ribs had been cut bilaterally and the viscera were held in place by strings tied around the body. When the strings were cut, the sternum fell out of the body! Shot damage to the specimen of *Dromococcyx* was so great that I could not study some important anatomical details. I made a plea several years ago (1955*a*) for better anatomical material. For the benefit of all students of pterylosis, myology, etc., I repeat that plea here. One often feels that it is better to have no representative of a species or genus than to have a specimen so mutilated by shot damage or by incisions that one can obtain only a portion of the information that one needs.

Anatomists sometimes are criticized for publishing information based on the dissection of only one or two specimens of a species. To be sure, the anatomist would be delighted to have a dozen or more specimens of each form that he is studying, but he is rarely so fortunate. In order to obtain the specimens that form the basis for this paper, I wrote well over a hundred letters to all parts of the world during a 12-year period. Perhaps this is the best example that I could cite to emphasize the continuing great need for well-preserved anatomical material.

Wing Muscles of *Tauraco leucotis donaldsoni*

M. latissimus dorsi.—*Pars anterior* arises from the neural spines of the last two cervical and the first dorsal vertebrae. It inserts fleshily over an area 7 mm. long beginning 9 mm. from the proximal end of the head of the humerus. *Pars posterior* arises from the neural spines of the five dorsal vertebrae. It inserts by a flat tendon (2 mm. wide) immediately posterior to the proximal end of the insertion of pars anterior. *Pars metapatagialis*, the dermal component, is a very small band of fleshy fibers about 1 mm. in width. It arises from the superficial surface of pars posterior at the level of the spine of dorsal vertebra number 4; it inserts into the skin at the posterior margin of the humeral feather tract adjacent to the insertion of M. serratus metapatagialis.

M. rhomboideus superficialis arises by an aponeurosis from the neural spines of the last three cervical and the first two dorsal vertebrae. The fleshy fibers pass outward and forward to insert on the anterior 36 mm. of the scapula.

M. rhomboideus profundus arises by an aponeurosis from the neural spines of the last two cervical and the first two dorsal vertebrae. The muscle inserts on the posterior 28 mm. of the scapula.

M. cucullaris, pars propatagialis.—I did not find any tendon of this muscle inserting on the tendon of the tensor patagii longus.

M. serratus profundus has a typical origin from the posterior cervical vertebrae and from the cervicodorsal ribs. The several fasciculi pass backward to insert on the medial surface of the scapula.

M. serratus anterior arises by a superficial and a deep band of fibers. The larger and more superficial slip arises from the lateral surface of the first true rib, ventral to the uncinate process. The deeper slip arises from the ventral portion of the last cervicodorsal rib. The two slips fuse and give rise to a strong aponeurosis (6 mm. wide), which passes upward between the two heads of M. subscapularis to insert on the ventral edge of the scapula just caudal to the glenoid fossa.

M. serratus posterior arises by fleshy fasciculi primarily from the uncinate processes of true ribs numbers 1, 2, and 3. The complex is an extensive, but thin, sheet of fleshy fibers that inserts on the apex of the scapula (by fleshy fibers) and on the ventral edge of that bone (by an aponeurosis) as far craniad as the insertion of M. serratus anterior. *Pars metapatagialis*, the dermal component, has a typical origin. The belly, about twice as large as pars metapatagialis of M. latissimus dorsi, passes upward to insert into the skin at the posterior margin of the humeral feather tract.

M. proscapulohumeralis is a thin strap of fleshy fibers 4 mm. wide at its origin from the scapula immediately posterior to the glenoid lip and the origin of M. scapulotriceps. The belly is about 13 mm. in length. It has a typical insertion on the humerus between the two heads of origin of M. humerotriceps.

M. dorsalis scapulae arises from the lateral surface of the scapula in its posterior 33 mm. It inserts on the anconal surface of the bicipital crest of the humerus.

M. subscapularis has the usual two heads.—*Pars externa* arises for a distance of 8 mm. from the ventrolateral edge of the scapula, beginning a short distance caudal to the glenoid fossa. *Pars interna* arises from an area about 20 mm. long on the medial surface of the scapula. The two heads fuse and insert by a short stout tendon on the internal tuberosity of the humerus, adjacent to the insertion of M. subcoracoideus.

M. subcoracoideus arises by two heads, a clavicular head and a coracoidal head. The clavicular head is unusually well developed. It has an extensive origin from an area 17 mm. long on the medial surface of the superior end of the clavicle and from the acromion of the scapula. The coracoidal head arises from the basal 10 mm. of the posterior face of the coracoid and from the adjacent coracoclavicular membrane. The two heads fuse and insert in common on the internal tuberosity of the humerus.

M. coracobrachialis anterior is a well-developed muscle, although it does not cover the anterior surface of the head of the humerus. It arises from the head of the coracoid (and adjacent ligaments) immediately dorsal to the origin of M. biceps brachii. The belly (about 13 mm. long and 5 mm. in maximum width) passes outward, closely applied to the capsule of the shoulder joint, to insert on the proximal end of the humerus.

M. coracobrachialis posterior has a typical origin and insertion.

M. supracoracoideus has a typical origin from the sternum and the coracoclavicular membrane. A very large tendon of insertion is formed; the fleshy fibers continue through the triosseal canal (see p. 82) with the tendon and cover it almost to the point of insertion on the humerus.

M. sternocoracoideus has a typical origin and insertion.

M. pectoralis.—*Pars thoracicus* is very well developed; it has a typical origin and insertion. *Pars propatagialis longus et brevis* is a large fleshy fasciculus arising from the ventral surface of pars thoracicus. The fleshy bundle fuses with the distal end of the belly

of M. tensor patagii longus, but it also gives rise to a flat bandlike tendon which appears to form the bulk of the tendon of M. tensor patagii brevis. The belly of the latter muscle appears to insert into the tendon formed from pars propatagialis. Near its formation, the tendon of pectoralis pars propatagialis has a tendinous anchor to the anterior edge of the deltoid crest of the humerus.

M. deltoideus major has a total length of belly (from the scapular origin) of about 44 mm.; the terminal tendinous insertion reaches to within 12 mm. of the distal end of the humerus. The longer head arises from the acromion of the scapula and by a strong aponeurosis from the ventral edge of that process, as in *Coua caerulea*. The much smaller anterior head arises from the very large os humeroscapulare; it inserts by fleshy fibers on the anconal surface of the deltoid crest.

M. deltoideus minor is, relatively, a fairly well-developed muscle in the touraco. It is a flat band of fleshy fibers 3 mm. wide and 14 mm. long. Unlike the origin in *Coua*, it arises from the acromion and from the coracoscapular and acromioclavicular ligaments. It has a typical insertion at the junction of the articular head and the deltoid crest of the humerus. The belly, which passes anterior to the os humeroscapulare and overlies the subjacent tendon of M. supracoracoideus, is visible anterior to M. deltoideus major after removal of Mm. tensores patagii longus et brevis.

Mm. tensores patagii longus et brevis are represented by a common belly which arises from the dorsal and medial surfaces of the apex of the clavicle and the tip of the acromion; posteriorly, the origin is shared with the posterior head of M. deltoideus major. The origin of this complex in *Tauraco leucotis* is like that found in the cuckoos and not like that illustrated for *Tauraco corythaix* by Lowe (1943). The insertion of the tensor patagii brevis seems to be similar in the two species, and I suspect that Lowe's separation of the tendon into two discrete slips in *corythaix* may have been an artifact. At any rate, in *leucotis* the tendon of the brevis is a single sheet (about 1.5 mm. wide) which inserts primarily into the belly of M. extensor metacarpi radialis, but an extension of this tendon-sheet proximally passes posteriorly over the forearm muscles to fuse with the antebrachial fascia, which is closely adherent to the bases of the proximal secondaries.

M. biceps brachii has a typical double origin from the coracoid and from the bicipital crest of the humerus. The belly, 37 mm. in length, extends to the distal end of the humerus. The tendon bifurcates to insert 2 mm. and 3 mm., respectively, from the proximal ends of radius and ulna. A biceps slip is not present.

M. triceps brachii exhibits about the same development as in the cuckoos. The scapulotriceps portion has a somewhat two-headed fleshy and tendinous origin: one head from the lateral surface of the scapula, dorsal to the glenoid fossa; the other head from the ventrolateral edge of the scapula just caudal to the glenoid lip. There is no humeral anchor. The humerotriceps can be divided into two heads only proximally, where the two heads arise on either side of the insertion of M. proscapulohumeralis. There is a typical insertion on the olecranon and the adjacent area on the proximal end of the ulna.

M. expansor secundariorum is similar in structure to that previously described for several cuckoos in that there is both a humeral and a scapular origin. The two tendons of origin give rise to fleshy fibers that insert on several of the proximal secondaries. The short tendon arises from the distal end of the humerus. The long tendon extends proximad through the metapatagial skin fold to the axilla where the tendon bifurcates. The dorsal branch attaches to the medial surface of the scapula, deep to the origin of M. subcoracoideus and at about the line of separation between this muscle and M. subscapularis (pars interna). The ventral branch attaches to the coracoid in relation to the origin of M. coracobrachialis posterior; this attachment I have not found in the cuckoos (see p. 77).

M. anconaeus coracoideus.—I did not find this muscle in the specimen I dissected.

M. brachialis is typical in origin and insertion.

M. pronator superficialis is a well-developed muscle (belly 35 mm. long) which extends to within 10 mm. of the distal end of the radius.

M. pronator profundus, with a belly 32 mm. long, extends distad almost as far as M. pronator superficialis. The origin of both muscles is typical.

M. flexor digitorum superficialis has a typical origin from the distal end of the humerus. The tendon of origin expands into a broad aponeurosis (the humerocarpal band) which extends the entire length of the ulna and fuses with the fascia around the bases of the secondaries; near the distal end of the ulna, the humerocarpal band gives rise to fleshy fibers (essentially a second belly for the muscle), which fuse with the main belly just before the tendon of insertion is formed. The main belly (30 mm. long) arises from the deep surface of the humerocarpal band, beginning 12 mm. from its humeral attachment. The muscle inserts on the base of the proximal phalanx of digit II.

M. flexor digitorum profundus arises by a single head from the ulna, posterior to the area of insertion of M. brachialis. The belly is about 33 mm. in length; it extends to the distal end of the ulna. The main tendon of insertion passes around the pisiform process of the carpometacarpus and then passes distad superficial to the tendon of the flexor digitorum superficialis to insert on an extensive area of the distal phalanx of digit II. A very unusual feature is the presence of a second tendon given off the main tendon opposite the base of the pollex; this tendon inserts on the palmar surface of the pollex.

M. flexor carpi ulnaris is a well-developed muscle, whose belly (37 mm. long) extends nearly the entire length of the forearm. The origin and insertion are typical, but fleshy fibers do not insert on the bases of the secondaries as they do in *Coua caerulea*.

M. extensor metacarpi radialis has a typical origin from the lateral epicondyle of the humerus. The belly is about 34 mm. long. The tendon of the tensor patagii brevis muscle inserts into the belly and its enveloping fascia about 10 mm. distal to the humerus. The tendon of M. extensor metacarpi radialis inserts on the extensor process of the carpometacarpus. M. abductor pollicis arises from the tendon a short distance before its insertion.

M. flexor metacarpi radialis arises by a tendon attached to the lateral epicondyle of the humerus. The belly is about 28 mm. long, and the fleshy fibers begin about 10 mm. from the humeral origin of the tendon. A fascial extension of the tendon of origin fuses with the fascia surrounding the bases of the proximal secondaries. The tendon inserts on metacarpal II, about 6 mm. from the proximal end of that bone at the proximal limit of the intermetacarpal space.

M. extensor digitorum communis arises by a tendon from the lateral epicondyle of the humerus. The fleshy fibers of the 33 mm.-long belly begin almost at the humeral origin of the tendon. Two tendons are formed near the base of the carpometacarpus. The shorter tendon inserts on the base of the pollex. The longer tendon runs in a groove on the dorsal surface of metacarpal II; near the distal end of that bone, the tendon turns abruptly around a bony tubercle to insert on the base of the proximal phalanx of digit II.

M. anconeus has a typical origin from the humerus. The belly (39 mm. long) extends nearly the entire length of the ulna.

M. supinator has a typical origin from the humerus. The belly is short (about 18 mm.), extending less than half the length of the radius, on which bone it inserts.

M. extensor indicis longus is a long (26 mm.), thin muscle arising from the radius only. Its tendon inserts on the base of the distal phalanx of digit II.

M. flexor metacarpi brevis is absent bilaterally.

M. flexor carpi ulnaris brevis is a short muscle, with a belly 13 mm. long, arising from

the ventral surface of the distal third of the ulna. The tendon has a typical insertion on the dorsal surface of the base of the carpometacarpus.

M. extensor pollicis longus is a well-developed muscle with two heads of origin; the over-all length of the belly is 34 mm. The smaller head (24 mm. long) arises from the middle half of the radius. The larger head (30 mm. long) arises from the ulna, beginning at the level of insertion of M. biceps brachii. The tendon inserts on the extensor process of the carpometacarpus deep to the tendon of M. extensor metacarpi radialis.

M. extensor pollicis brevis is a triangular muscle with two heads of origin and with a total length of about 6 mm. The larger head arises from the base of the carpometacarpus. The smaller head arises from the base of the extensor process and from the tendon of insertion of M. extensor pollicis longus.

M. abductor pollicis, with a single belly 6 mm. long, has a typical origin from the tendon of insertion of M. extensor metacarpi radialis. It inserts by fleshy fibers on the pollex.

M. adductor pollicis arises fleshily from the anterior surface of the carpometacarpus near the base of the extensor process. It inserts by fleshy fibers on the posterior face of the pollex.

M. flexor pollicis is a very small band, less than 1 mm. in width, which arises from the carpometacarpus; it inserts on the base of the pollex, posterior and adjacent to the insertion of M. abductor pollicis.

M. abductor indicis is a well-developed muscle, arising from an extensive area on the base of the carpometacarpus, both anterior and posterior to the pisiform process, and from nearly the entire length of the anterior surface of metacarpal II. The muscle inserts by a stout tendon on the anterior surface of the proximal phalanx of digit II.

M. flexor metacarpi posterior has a typical origin by a strong flat tendon from the distal end of the ulna. The well-developed belly inserts on the posterior surface of about the proximal half of metacarpal III, and it also sends fleshy fasciculi into the bases of the proximal five or six primaries.

M. flexor digiti III arises along a narrow line from most of the palmar surface of metacarpal III, beginning at the proximal limit of the intermetacarpal space, and from the posterior surface of that same bone distal to the insertion of M. flexor metacarpi posterior. The muscle inserts by a tendon on the base of digit III and by fleshy fibers on the entire anconal surface of that digit.

Mm. interossei dorsalis et palmaris have typical origins from the facing surfaces of metacarpals II and III. M. interosseus dorsalis inserts by a tendon on the base of the distal phalanx of digit II. M. interosseus palmaris inserts by a tendon a little beyond mid-length of the distal phalanx of digit II.

"Leg" Muscles of *Tauraco leucotis donaldsoni*

M. sartorius arises from the anterodorsal end of the ilium only, i.e., it has no origin from the neural spine of the last dorsal vertebra. It inserts on the anteromedial corner of the head of the tibiotarsus.

M. iliotibialis is a very extensive muscle, covering all other muscles on the lateral aspect of the thigh except for parts of Mm. sartorius and semitendinosus. The central part of the complex is aponeurotic in its distal three-fifths. The muscle arises from the anterior iliac process and from the entire length of the anterior and posterior iliac crests. Most of the origin is by an aponeurosis (including that from the anterior iliac process), but the origin posteriorly is by fleshy fibers. Anteriorly, the origin is inseparably fused with the origin of M. sartorius. Distally, the tendon contributes to the formation of the patellar

ligament, inserts on the tibiotarsus, and fuses with the deep fascia of the crus, particularly that covering M. peroneus longus.

M. iliotrochantericus posterior is well developed and has a considerable bulk of its fibers arising dorsal to the acetabulum. The muscle arises from the anterior iliac process and from all of the anterior iliac fossa. It inserts on the femur by a strong flat tendon, beginning 1 mm. distal to the trochanter.

M. iliotrochantericus anterior also is well developed. It arises from the posterior surface of the anterior iliac process and from the ventrolateral edge of the ilium. It inserts by a strong tendon (2 mm. wide) on the lateral surface of the femur, beginning 7 mm. distal to the proximal end of that bone.

M. iliotrochantericus medius is absent bilaterally.

M. gluteus medius et minimus is conspicuously developed, especially the long tendon of insertion, which passes superficial to the tendon of M. iliotrochantericus posterior to insert on the posterolateral edge of the femur about 7 mm. from the proximal end of that bone between the areas of insertion of Mm. iliotrochantericus anterior and ischiofemoralis. The fleshy belly is 5 mm. long; it arises from the most posterior part of the anterior iliac crest.

M. femorotibialis externus arises by fleshy and semitendinous bands (especially distally) from most of the lateral surface of the femur. The origin begins just distal to the level of insertion of M. iliotrochantericus anterior.

M. femorotibialis medius arises by tendinous and fleshy fibers from the trochanteric ridge and the femoral shaft distal to it. The belly is fused with that of M. femorotibialis externus. Both muscles contribute to the patellar ligament; their configuration is like that illustrated for *Coua caerulea* (Berger, 1953*a*: Fig. 6).

M. femorotibialis internus is a long thin muscle that arises from the medial surface of the femur, beginning 14 mm. inferior to the neck of that bone; the belly increases in size distally. It inserts by a single tendon on the anteromedial surface of the head of the tibiotarsus.

M. biceps femoris arises by two heads which fuse at about mid-thigh level. The anterior head is somewhat larger; it arises by an aponeurosis from the caudal portion of the anterior iliac crest and by fleshy fibers from the anterior 3 mm. of the posterior iliac crest. The more rounded posterior head arises by tendinous and fleshy fibers from a pronounced tubercle on the lateral surface of the ilium about 3 mm. ventral to the projecting posterior iliac crest. The muscle inserts by a stout, rounded tendon on the fibula about 16 mm. inferior to the head of that bone.

M. ischiofemoralis has a typical origin from the lateral surface of the ischium, dorsal to the origins of Mm. semimembranosus and adductor longus et brevis. It inserts by a strong tendinous band (2.5 mm. wide) beginning 5 mm. inferior to the trochanter and immediately posterior to the insertion of M. gluteus medius et minimus.

M. piriformis.—Both parts of this complex are well developed. *Pars caudofemoralis* arises from the base of the pygostyle by a wide (8 mm.) tendinous band and by fleshy fibers from the superficial surface of this band. The maximum width of the belly, inferior to the posterior iliac crest, is 10 mm. *Pars iliofemoralis* arises by fleshy fibers from the lateral surface of the ilium, ventral to the origin of Mm. semitendinosus and biceps femoris. The belly passes downward and forward, superficial to pars caudofemoralis, to insert on the posterolateral edge of the femur for a distance of 7 mm., beginning 10 mm. inferior to the trochanter. Pars caudofemoralis inserts by a tendon-sheet (4.5 mm. wide), beginning 12 mm. inferior to the trochanter and immediately medial to and in contact with the insertion of pars iliofemoralis.

Mm. semitendinosus and *accessorius semitendinosi.*—The bulky semitendinosus muscle

arises from the ventral surface of the projecting posterior iliac crest in its posterior 8 mm.; there is no origin from the free caudal vertebrae. The raphe which separates this muscle from the accessory semitendinosus muscle behind the knee broadens into a 2 mm.-wide tendon, which inserts on the medial surface of the tibiotarsus 2 mm. posterior to the insertion of M. semimembranosus. The accessorius muscle inserts by fleshy fibers on the posterolateral edge of the femur in its distal 13 mm.

M. semimembranosus arises by an aponeurosis (shared in part with M. adductor longus et brevis, pars externa) attached to the lateral surface of the ischium a few millimeters dorsal to the ischiopubic fenestra. Most of the thin sheetlike belly of the semimembranosus muscle is concealed by the overlying semitendinosus muscle. M. semimembranosus inserts along a curved line (6 mm. long) on the anteromedial edge of the tibiotarsus, beginning 7 mm. inferior to the proximal end of that bone.

M. iliacus.—I found no evidence of this muscle in either leg.

M. ambiens is a thin strap of muscle, 30 mm. in length; it has a maximum width of 5 mm. near its origin from the pectineal process. It arises mostly by fleshy fibers. The tendon of insertion, like that in *Coua caerulea*, enters the patellar ligament and passes diagonally downward and laterad around the front of the knee. Below the knee the tendon fans out into an aponeurosis which gives origin to parts of Mm. flexores perforati digiti II, III, and IV.

M. obturator internus is a well-developed triangular-shaped muscle arising from the medial surface of the ischium and pubis; it also has a large portion arising in the renal depression, as in *Coua* and several other unrelated birds. The large tendon passes out of the obturator foramen and inserts on the lateral surface of the femur, proximal to the insertion of M. ischiofemoralis and beginning about 3 mm. inferior to the trochanter. The tendon of M. gluteus medius et minimus passes superficial to the tendons of insertion of Mm. obturator internus and externus.

M. obturator externus is a small band of fleshy fibers arising from the dorsal margin of the obturator foramen. A flat tendon forms and fuses with the proximal side of the tendon of M. obturator internus.

M. adductor longus et brevis is composed of two distinct parts. *Pars externa* arises by an aponeurosis (8.5 mm. wide) from the lateral surface of the ischium, beginning about 2 mm. caudal to the obturator foramen and 4 mm. dorsal to the ischiopubic fenestra. Pars externa inserts on the femur medial to M. piriformis and beginning at the inferior limit of the tendon of pars caudofemoralis and extending distad about 23 mm. *Pars interna* arises by a dense aponeurosis 10 mm. wide, beginning at the posterior margin of the obturator foramen and passing caudad along the dorsal margin of the ischiopubic fenestra. Fleshy fibers form at once in the anterior fifth, but posteriorly the aponeurosis extends distad about 15 mm. before fleshy fibers arise. Pars interna inserts on the femur mostly by an aponeurosis (by fleshy fibers superiorly), medial to the insertion of pars externa and extending for a distance of 33 mm.

M. tibialis anterior, as in other birds, has both a femoral and a tibial head. The femoral head arises by a stout tendon from the anterodistal end of the external femoral condyle. The tibial head arises in common with, but deep to, M. peroneus longus. The two heads fuse about a third the way down the crus. The over-all length of the belly is 60 mm., and it extends distad as far as the ligamentum transversum. A very large tendon of insertion is formed; it passes deep to the ligamentum transversum and inserts 7 mm. inferior to the proximal end of the tarsometatarsus. Just before the area of insertion, the tendon gives off a fascial band that fuses with the fascia covering the muscles of the anterior surface of the tarsometatarsus.

M. extensor digitorum longus arises by fleshy fibers from the proximal third of the anterior surface of the tibiotarsus and from the inner and outer cnemial crests of that bone. The belly extends for a distance of 60 mm., but the muscle is very small in its distal half. The tendon passes deep to the ligamentum transversum and then under a bony bridge on the anterior surface of the tibiotarsus. Continuing distad, the tendon is held in place by a strong ligament (and not by a bony bridge) on the proximal end of the tarsometatarsus. The tendon trifurcates in the distal third of the tarsometatarsus to supply digits II, III, and IV. The tendon complex to digit III (the largest digit) is unusually well developed; the small single tendon to digit II exhibits the poorest development. Attachments of the tendons are made to each of the phalanges of the respective digits.

M. peroneus longus arises by semitendinous bands, in common with the underlying muscles, from the outer and inner cnemial crests and the rotular crest of the head of the tibiotarsus. The belly is about 50 mm. long, and, although it covers all of the other muscles on the anterolateral surface of the proximal five-sevenths of the crus, it is a relatively thin sheet of muscle which does not extend around to the medial surface of the crus (as this muscle does in *Coua*). The tendon bifurcates near the distal end of the tibiotarsus. The shorter of the two tendons inserts on the tibial cartilage and associated ligaments. The longer tendon passes downward to insert on the tendon of M. flexor perforatus digiti III a short distance inferior to the proximal end of the tarsometatarsus.

M. peroneus brevis arises from the fibula and the tibiotarsus for a distance of about 45 mm., beginning at the level of insertion of M. biceps femoris. It inserts on the posterolateral corner of the proximal end of the tarsometatarsus at the base of the hypotarsus.

M. gastrocnemius has the typical three heads. *Pars externa* arises primarily by a flat aponeurotic band fused to the lateral surface of the distal arm of the biceps loop. *Pars media* arises from the posterior surface of the distal end of the femur, immediately distal to the area of insertion of M. accessorius. *Pars interna* arises from the entire medial surface of the inner cnemial crest of the tibiotarsus and from the fascia covering the anterior and medial aspects of the knee joint, where this head has an intimate relationship to the fleshy insertion of M. sartorius. None of pars interna covers the anterior or lateral portion of the crus, as it does in *Coua caerulea*. Pars media and pars interna are separated by the tendon of insertion of M. semimembranosus. There is also a strong fascial band extending from M. semitendinosus to both pars media and pars interna. The very strong common tendon of M. gastrocnemius inserts on the back of the hypotarsus and the posterior ridges of the tarsometatarsus throughout most of its length.

M. plantaris has a typical origin from the proximal end of the tibiotarsus. The belly is about 18 mm. in length. The small tendon of insertion expands distally and inserts on most of the proximal end of the tibial cartilage.

M. popliteus is a reasonably well-developed muscle, about 3 mm. wide and 6 mm. long. Both the origin and the insertion are semitendinous. It arises from the head of the fibula. The fleshy fibers pass downward and mesiad to the insertion on the tibiotarsus.

M. flexor perforatus digiti II is a small muscle with a belly 35 mm. long but only 3 mm. wide. It arises from the continuation of the ambiens tendon and from the deep surface of M. flexor perforatus digiti III. The tendon passes through the deep aspect of the lateral side of the tibial cartilage. The tendon of insertion is perforated by both of the deep flexor tendons to digit II (flexor digitorum longus and flexor perforans et perforatus digiti II) and then inserts on both sides of the proximal phalanx of digit II.

M. flexor perforatus digiti III arises from the femur (in common with Mm. flexor perforatus digiti IV and flexor hallucis longus) and from a broad aponeurosis which is a continuation of the ambiens tendon. The belly is 50 mm. in length. The long tendon of

M. peroneus longus inserts on the tendon about 8 mm. inferior to the proximal end of the tarsometatarsus. Near the distal end of the tarsometatarsus, the tendon is united by a vinculum ("V") with the tendon of M. flexor perforans et perforatus digiti III, which lies deep to the tendon of M. flexor perforatus digiti III. The vinculum arises from the deep surface of the latter tendon and then passes deep to the subjacent tendon of flexor perforans et perforatus digiti III, so that the vinculum fuses with the deep side of the latter tendon. The very large tendon of insertion of M. flexor perforatus digiti III is perforated by both of the deep flexor tendons to digit III and then inserts on both sides of the proximal phalanx and on the base of the second phalanx of digit III.

M. flexor perforatus digiti IV arises from the femur (in common with Mm. flexor perforatus digiti III and flexor hallucis longus) and from the ambiens tendon. The belly is 40 mm. in length. At the base of digit IV, the tendon of flexor perforatus digiti IV expands into a large mass, which ensheathes the tendon to that digit of M. flexor digitorum longus. The tendon then sends slips to attach to the proximal ends of phalanges 2, 3, and 4 of digit IV.

M. flexor perforans et perforatus digiti II appears to arise exclusively from the lateral femorofibular ligament (i.e., there is no direct origin from bone), immediately distal to the attachment of the distal arm of the biceps loop. The belly is 22 mm. long. The tendon inserts on both sides (the medial slip being the stronger) of the bones at the interphalangeal joint between phalanges 1 and 2 of digit II.

M. flexor perforans et perforatus digiti III arises by fleshy and tendinous fibers from the outer cnemial crest, the third arm of the biceps loop, and from adjacent ligaments on the anterolateral aspect of the knee, including the patellar ligament. The belly is about 40 mm. long. The tendon perforates the tendon of M. flexor perforatus digiti III and is itself perforated by the tendon of M. flexor digitorum longus. It inserts on both sides of the distal end of phalanx 2, digit III.

M. flexor digitorum longus arises by two distinct heads from the proximal end of the tibiotarsus, most of M. popliteus being visible between the two heads. The belly (55 mm. long) extends to within 15 mm. of the distal end of the tibiotarsus, so that this muscle is very well developed as compared with M. flexor hallucis longus. The tendon of M. flexor digitorum longus is the only one that passes through a bony canal in the hypotarsus. Inferior to that process, the tendon of the flexor hallucis longus passes diagonally downward and superficial to the tendon. The two tendons are connected by a small vinculum in the distal fourth of the tarsometatarsus. The tendon of the flexor digitorum longus muscle trifurcates. The primary insertion of each branch is on the ungual phalanx of digits II, III, and IV. Vinculae pass from the deep surface of the tendons to other phalanges of these digits.

M. flexor hallucis longus is, compared with the flexor digitorum longus, a weakly-developed muscle with an over-all belly-length of about 30 mm. It arises by two distinct but short heads from the distal end of the femur; both heads lie medial to the tendon of M. biceps femoris. The more lateral (anterior of Hudson, 1937:49) and fleshy head arises from the posterior face of the external condyle. The larger medial head arises by tendinous fibers from the intercondyloid area of the femur; this origin is shared with Mm. flexores perforati digiti III and IV. The tendon of insertion *does not* pass through a bony canal in the hypotarsus, but passes along the lateral surface of that process, where it is held in place by a fascial band. The tendon inserts on the ungual phalanx of the hallux.

M. flexor hallucis brevis is a bulky muscle whose belly (15 mm. long) is limited to the proximal third of the tarsometatarsus. The tendon expands to ensheath the tendon of M.

flexor hallucis longus and then inserts on both sides of the base of the proximal phalanx of the hallux.

M. extensor hallucis longus arises by two heads, one on each side of the tendon of insertion of M. tibialis anterior. The medial head is the larger of the two. The origin begins at the proximal end of the tarsometatarsus. The over-all length of the belly is 15 mm. The tendon is held in place by fibrous bands at the distal end of the tarsometatarsus. The single tendon inserts on the base of the ungual phalanx of the hallux.

M. extensor proprius digiti III is a long, thin and weakly-developed muscle, whose belly begins at the proximal end of the tarsometatarsus between M. extensor brevis digiti IV and the tendon of M. tibialis anterior. The tendon forms at the junction of the proximal and middle thirds of the tarsometatarsus. Fleshy fibers insert on this tendon to the level of the trochlea for digit III, so that the over-all length of the fleshy belly is 35 mm. The tendon expands to insert on most of the dorsal surface of the proximal phalanx of digit III.

M. extensor brevis digiti IV is another long, thin muscle, whose origin begins at the proximal end of the tarsometatarsus and extends distad about 32 mm. The tendon passes around the trochlea for digit IV and inserts on the medial side of the base of the proximal phalanx of that digit.

M. abductor digiti II is a fairly stout muscle, 10 mm. long, which arises from the distal end of the tarsometatarsus. It inserts by a tendon on the dorsomedial corner of the base of the proximal phalanx of digit II. The tendon is visible throughout its course.

M. lumbricalis is vestigial. A few fleshy fibers (about 7 mm. in length) arise from the deep side of the tendon of M. flexor digitorum longus near the distal end of the tarsometatarsus.

M. abductor digiti IV has a small belly 10 mm. long, which is limited to the proximal end of the tarsometatarsus. The long tendon is held in place by a ligament at the distal end of that bone. The tendon inserts on the ventrolateral corner of the base of the proximal phalanx.

Comparative Myology

My reasoning in the analysis that follows may be clearer if prefaced by some general remarks. If we assume with Hudson (1937:77) that the generalized condition is represented in those birds that possess the full complement of formulae and other muscles (as in the Galliformes), it follows that the absence of muscles represents a specialized condition. We assume also that, by and large, closely related birds will have lost the same muscles, and that either the hypertrophy or the loss of leg muscles must in general be correlated with locomotor habits or feeding habits (as in the birds of prey, with their very large flexor digitorum longus and flexor hallucis longus muscles). Further, we recognize that the age of a genus (and/or its geographical isolation and related factors) may be such that differences in locomotor pattern within the genus may not yet be accompanied by extensive myological changes. Finally, we assume that what we refer to as a "vestigial muscle" is a muscle that is in the process of being lost phylogenetically, that the degree of degeneration of such a muscle may vary among individual specimens of a genus or a species, and that one might expect some individual variation in the presence or absence of such a vestigial muscle.

Lowe (1943:512–514) made a considerable issue out of the alleged difference in development of M. iliotibialis between *Tauraco corythaix* and *Cuculus canorus*. I have been puzzled by the fact that I could not in any sense corroborate Lowe's description and illustration of M. iliotibialis in *Cuculus*. Actually, there is little resemblance between Lowe's figure of this muscle in *Cuculus* and what I found in the specimens available for dissection. Except for the fact that the central portion of this muscle is not aponeurotic from origin to insertion, M. iliotibialis in *Cuculus* is very similar to that muscle in *Chrysococcyx* ("*Lampromorpha*") *caprius* (Berger, 1955*b*: Fig. 71), and it is almost identical to the muscle in *Ch. cupreus* (Fig. 1).

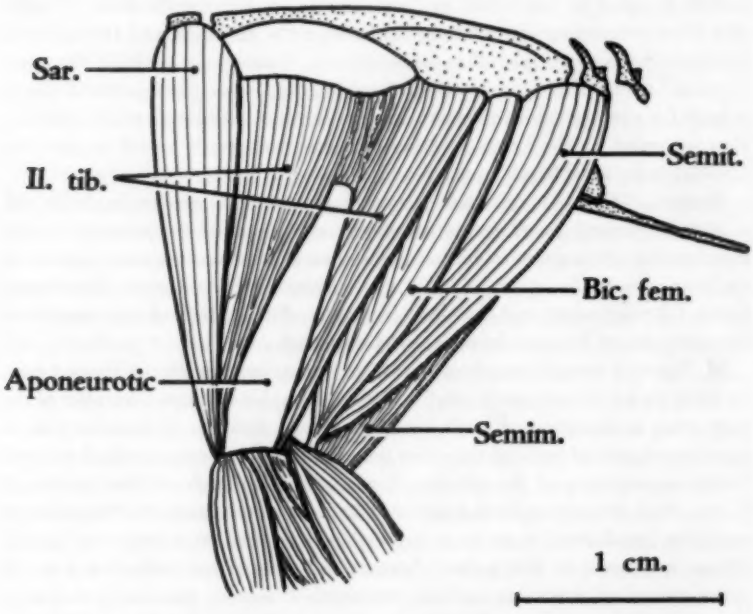

FIG. 1. Lateral view of thigh of *Chrysococcyx cupreus* to illustrate the relative weak development of M. iliotibialis. Bic. fem., biceps femoris; Il. tib., iliotibialis; Sar., sartorius; Semim., semimembranosus; Semit., semitendinosus.

In *Cuculus*, M. iliotibialis arises by fleshy fibers from the tip of the anterior iliac process and by an aponeurosis from the anterior iliac crest and the cephalic half of the posterior iliac crest. The caudal part of this aponeurosis

overlies the origin of the anterior portion of M. biceps femoris (as in other cuculine genera), but the iliotibialis muscle has no direct attachment to the belly of the biceps muscle (as illustrated by Lowe). The posterior segment (the gluteus posterior of Gadow) of the iliotibialis muscle is poorly developed so that it does not conceal any part of Mm. semitendinosus or semimembranosus, and it conceals only a small proximal and anterior part of M. biceps femoris. The central portion of the iliotibialis muscle is aponeurotic in about its distal half, and few, if any, of the fleshy fibers of the relatively small anterior and posterior fleshy parts of the complex extend distad as far as the knee. Relative to other cuckoos, M. iliotibialis is poorly developed in *Cuculus* and in *Chrysococcyx*. In many cuckoos, however, the development of M. iliotibialis is equal to that found in *Tauraco*. Hence, this muscle does not offer any clues concerning the relationship between the touracos and the cuckoos. It might be well to add that, anatomically, *Cuculus* is perhaps the least "typical" genus of the family, and, therefore, that it is a poor genus to use as a basis for comparison with genera of other families. Although much information is needed on the habits of other parasitic cuckoos, it would appear that *Cuculus* is the most highly specialized genus in the family.

Hudson (1937:14) reported that among American genera of birds, M. iliacus is "present in all forms examined and is one of the most uniformly developed thigh muscles in birds." This muscle is present in some genera of cuckoos, absent in other (Old World) genera: *Carpococcyx, Centropus, Coua, Chrysococcyx,* and *Cuculus*. Moreover, I did not find this muscle in the specimen of *Tauraco leucotis* that I dissected.

M. iliacus is a small muscle at best (with a maximum width of about 1 mm. in most cuckoos examined), and it might easily be destroyed by shot or be torn away in dissecting. Except for *Carpococcyx*, however, I dissected two or more specimens of each of the other genera of cuckoos mentioned above and found no evidence of the muscle; it was absent in each of five species of *Coua*. Shot damage to both femora of the single specimen of *Dromococcyx* available for dissection made it impossible to determine whether or not M. iliacus is present in that genus. Because this muscle has been found in all other genera of American cuckoos examined, I assume tentatively that it is present in *Dromococcyx*. Relative to other muscles in the thigh, M. iliacus might well be considered vestigial or rudimentary (with a very weak action) in many birds. It is highly desirable for someone to conduct a study directed to determine whether or not the absence of this muscle within a genus or species is a matter of individual variation. Gadow and Selenka (1891:145) reported that M. iliacus was absent as an individual variation in *Bucorvus* and *Platycercus*.

Nevertheless, I have proposed (1959) that M. iliacus be included in leg-

muscle formulae and that its presence be indicated by adding the letter "E" to such formulae. I would be among the first to agree that muscle formulae must be used with caution and that they often are misused. I think that this is especially the case when contemporary writers ignore data presented by Hudson and others and include only the symbols proposed many years ago by Garrod. Thus, if we use only Garrod's symbols, the muscle formula for *Tauraco leucotis* is ABXYAm; that for cuckoos is either ABXYAm or AXYAm. This is misleading because it does not tell the whole story; the myology of the hind limb is not that similar in the two groups of birds. This can be demonstrated by using Hudson's expanded muscle formula, with or without the addition of "E." The formula for *Tauraco* then becomes ABDXYAmV. For cuckoos the formulae are:

AXYAm—*Cuculus, Chrysococcyx*

AEXYAm—*Coccyzus, Piaya, Saurothera, Tapera, Clamator, Surniculus*

ABXYAm—*Coua, Carpococcyx, Centropus*

ABEXYAm—*Geococcyx, Morococcyx, Dromococcyx* (E?), *Crotophaga, Guira, Ceuthmochares, Phaenicophaeus*

It is my opinion that the presence of M. gluteus medius et minimus (D) and of the vinculum (V; between the tendons of Mm. flexor perforatus digiti III and flexor perforans et perforatus digiti III) in *Tauraco* and the absence of these structures in the cuckoos constitute a significant difference in their pelvic musculature. Another interesting difference is that in the cuckoos the two deep plantar tendons (the tendons of Mm. flexor digitorum longus and flexor hallucis longus) pass through separate bony canals in the hypotarsus, whereas in *Tauraco* there is a single bony canal that transmits only the tendon of M. flexor digitorum longus. M. flexor hallucis longus in *Tauraco* arises from the femur by two separate heads, both of which lie medial to the tendon of M. biceps femoris; in the cuckoos (but apparently not in *Centropus*) the muscle arises by a single head from the intercondyloid area of the femur.

Beddard (1898*a*:45) said that W. A. Forbes found the flexor hallucis longus muscle to be "totally absent" in *Centropus* (see also Verheyen, 1956*a*: 8), but I found it in both species examined. Beddard (1898*b*:276) further stated that the deep plantar tendons of *Centropus* are peculiar in that "no branch is sent to the hallux," and I found this to be true. M. flexor digitorum longus in *Centropus* is at least twice as bulky as M. flexor hallucis longus, although the latter muscle extends distad about half the length of the tibiotarsus. The tendons of both muscles pass through bony canals in the hypotarsus, below which the tendon of M. flexor hallucis longus fuses completely with the tendon of M. flexor digitorum longus. The resulting common tendon trifurcates to send branches to insert on digits II, III, and IV; *no branch is sent to the hallux.* There exists, however, a most unusual condition that I

have not seen in any other genus. There is a very large automatic flexor of the hallux (Berger, 1953*a*:75). From its attachment to the trochlea and the fibrocartilaginous pulley for digit IV, the automatic flexor passes mesiad to the base of the hallux and then runs distad (held close to the bone by a vaginal sheath) to insert on the entire *plantar* surface of the base of the distal phalanx of the hallux. Consequently, the relationships of the automatic flexor to the phalanges in *Centropus* are identical to those of the flexor hallucis longus tendon when it is present as in the other cuckoos. The absence of the tendon of M. flexor hallucis longus to the hallux in *Centropus* is compensated for, in part, because M. extensor hallucis longus not only has a typical insertion on the dorsal surface of the distal phalanx but it also sends a strong slip to insert on the medial and plantar edge of the proximal phalanx of the hallux (for other examples of this double insertion, see Hudson, 1937:52).

The absence of pars iliofemoralis (B) of M. piriformis (=M. caudofemoralis) in some of the cuckoos raises interesting questions. The muscle is absent in the more arboreal members of the group; it is present in the more terrestrial members (but also in *Eudynamis*). In locomotor habits, *Guira* and *Crotophaga* are intermediate between the cursorial *Geococcyx* and the arboreal *Coccyzus*. Both *Guira* and *Crotophaga* possess the full cuculine complement of leg muscles, and they also share similar social nesting habits. In this instance, therefore, the similarity in development of leg muscles would seem to indicate closeness of relationship rather than locomotor pattern. I assume that the primitive cuckoos possessed both parts of the piriformis complex and that the loss of pars iliofemoralis in certain modern cuckoos is a secondary condition correlated with locomotor habits, in this instance with perching and arboreal habits (often also with parasitic breeding habits). One disadvantage of muscle formulae, however, is that they indicate nothing about the relative development of the muscles concerned. It is interesting to note, for example, that in *Ceuthmochares* (unlike any of the other genera possessing the muscle) pars iliofemoralis is vestigial; it is a minute band of fleshy fibers about 1 mm. in width. One might expect this muscle to be absent, either unilaterally or bilaterally, in some specimens of *Ceuthmochares*. As a possible similar example, I have pointed out elsewhere (1956:436) that pars caudofemoralis of the piriformis complex may be considered to be vestigial in the Sandhill Crane (*Grus canadensis tabida*), and Fisher and Goodman (1955:86) reported that pars caudofemoralis was absent in one of three specimens of the Whooping Crane (*G. americana*). In the cuckoos, pars caudofemoralis is relatively well developed in all species examined, although it is more strongly developed in the arboreal species. (For a discussion of the function of pars caudofemoralis, see Fisher, 1957.)

The relative development of Mm. peroneus longus and peroneus brevis in

birds has been discussed by Mitchell and by Hudson (1937). Mitchell (1913: 1068) said: "I find it extremely difficult to associate the conditions of the peroneal muscles with differences in habit that point directly to functional adaptation," and that, with very few exceptions, "there is a close conformity between the condition of the peroneals and what appears to be the most securely founded systematic divisions. Birds seem to have this or that type of peroneal muscle, not because they are arboreal or terrestrial, swimmers or waders, scratchers, predatory or vegetarian, but because it is the type occurring in this or that systematic division."

One might agree in essence with such a generalization, but an analysis of these two muscles as found in the cuckoos may give one an insight into the difficulties involved as one attempts to determine which myological characters indicate closeness of relationship and which are a reflection of locomotor or other habits. These two factors are, of course, undoubtedly interrelated.

We may ignore for present purposes the fact that either of the peroneal muscles may be absent in a few non-cuculine genera. Among the cuckoos, then, we may say that M. peroneus longus exhibits its two extremes of development. At its highest degree of development, M. peroneus longus arises from the proximal end of the tibiotarsus, and its belly (or aponeurosis of origin) conceals all but the most distal parts of Mm. tibialis anterior and peroneus brevis (Berger, 1953*a*: Figs. 5, 8). This situation is found, in general, in terrestrial cuckoos (*Geococcyx, Morococcyx, Centropus, Carpococcyx, Coua, Crotophaga, Guira, Tapera*, and (?) *Dromococcyx*), but also in *Tauraco*. In a second group of primarily arboreal cuckoos, M. peroneus longus is a long, thin, and deeply situated muscle, concealing no part of M. tibialis anterior (Berger, 1952: Pl. II). This condition is found in *Coccyzus, Piaya, Saurothera, Ceuthmochares, Clamator, Chrysococcyx, Cuculus, Surniculus*, and *Phaenicophaeus*. With one exception (*Tapera*), the fully-developed peroneus longus muscle is found in those genera that possess both parts (AB) of M. piriformis. These genera either are essentially cursorial and terrestrial birds or they are well-defined genera whose distribution or breeding behavior appear to set them apart from the remaining cuckoos. Among the cuculine genera considered in this paper, we may conclude that the relative development of M. peroneus longus coincides reasonably well both with locomotor habits and with the two major subgroups of the family. The relative development of this muscle, however, is of no value in determining the relationship between the cuckoos and the touracos (as Lowe proposed, 1943:514).

The relative development of M. extensor proprius digiti III seems to be correlated with locomotor habits. In the more arboreal cuckoos (and in *Tauraco*) this muscle arises just distal (just proximal in *Tauraco*) to the insertion of M. tibialis anterior, and the belly extends to the distal end of the

tarsometatarsus: *Coccyzus, Piaya, Saurothera, Crotophaga, Guira, Ceuthmochares, Surniculus, Clamator, Phaenicophaeus, Chrysococcyx, Cuculus.* In a second group, the entire muscle is limited to the distal half or less of the tarsometatarsus: *Geococcyx, Morococcyx, Dromococcyx, Tapera, Carpococcyx, Coua, Centropus.*

M. adductor digiti II is the smallest muscle of the pelvic limb in cuckoos. It seems proper to refer to it as a vestigial muscle in this group; it was, however, present (or absent) constantly in all specimens of the several genera examined. I did not find this muscle at all in *Cuculus, Chrysococcyx, Ceuthmochares, Surniculus, Phaenicophaeus, Centropus, Piaya,* or in *Tauraco.*

Certain tendon relationships in the foot appear to be correlated, in part, with zygodactylism, but there are curious exceptions. For example, the tendon of M. flexor perforatus digiti IV does not ensheathe the tendon of M. flexor digitorum longus in 16 of the genera studied, but it does ensheathe the longus tendon in *Dromococcyx* and in *Phaenicophaeus,* as well as in the semizygodactylous (see Moreau, 1938:666) *Tauraco. Phaenicophaeus* presents an intermediate condition in that about 95 per cent of the tendon inserts on the lateral side of the basal phalanx of digit IV, whereas the remainder of the tendon inserts on the medial side of the same phalanx. The tendon of M. flexor hallucis brevis forms a complete sheath around the tendon of M. flexor hallucis longus in all of the cuculine genera (as well as in *Tauraco* and many other birds) except *Centropus,* in which genus the flexor hallucis longus muscle does not insert on the hallux (see p. 73).

Another curious difference is found in the structure of M. femorotibialis internus in *Cuculus* and *Coua,* two distantly related cuckoos. In these two genera alone, M. femorotibialis internus has two independent heads, each of which inserts by its own tendon on the head of the tibiotarsus. The muscle is single in the other genera, including *Tauraco.*

Turning our attention now to the muscles of the wing, we find that Mm. tensores patagii longus et brevis in cuckoos (as in *Tauraco*) tend to be represented by a single muscle mass that gives rise to two tendons distally. There is a single fleshy origin from the dorsomedial surface of the furculum, also from the adjacent acromion of the scapula in some genera. In *Chrysococcyx* two bellies are discrete distally but the complex does not differ significantly from that in other cuckoos. The primary insertion of M. tensor patagii brevis in all cuculine genera (despite Lowe's statement and illustration) is on the tendinous surface of M. extensor metacarpi radialis, and part of the brevis tendon fans out posteriorly over the forearm muscles to fuse with the antebrachial fascia; the pattern is the same in *Tauraco* (see page 63, and Garrod, 1881, Pl. 22). There are secondary attachments of the brevis tendon-complex as follows: (1) to the lateral supracondylar ridge of the humerus—

Geococcyx; (2) to the lateral epicondyle (ectepicondylar process) of the humerus, superficial or proximal to the origin of M. extensor metacarpi radialis—*Coccyzus*; (3) to the tendon of origin of M. extensor digitorum communis—*Coccyzus, Morococcyx, Dromococcyx, Tapera, Chrysococcyx*. One must conclude that these secondary attachments are not important taxonomically.

M. expansor secundariorum has both a humeral and a scapular tendon of origin in all of the cuckoos. At the elbow there may be two independent bellies (as in *Coua, Geococcyx, Guira*, etc.) or a single muscle mass with two fleshy tongues directed proximally (as in *Crotophaga, Dromococcyx, Surniculus, Phaenicophaeus*) to the two primary (humeral and scapular) tendons of origin. This muscle is similar in *Tauraco*, but the axillary tendon bifurcates, the two resulting branches attaching respectively on the scapula and on the coracoid, i.e., the pattern of attachment is "ciconine" rather than "cuculine" (Garrod, Beddard). It seems likely that this is a significant difference between *Tauraco* and the cuckoos.

M. flexor metacarpi brevis is a small muscle, arising from the base of the carpometacarpus or from the os radiale and associated ligaments, and inserting on the tendon of insertion of M. extensor indicis longus. M. flexor metacarpi brevis is absent in *Coua, Carpococcyx, Geococcyx*, and *Morococcyx* (as well as in *Tauraco*); it is present in all other cuckoos examined. It should be noted that this muscle is present in all parasitic cuckoos and in all of those that lack pars iliofemoralis of the piriformis muscle. It is present also in *Crotophaga, Guira*, and in *Ceuthmochares* (in which genus pars iliofemoralis is vestigial); it is present but very much reduced in size in *Phaenicophaeus*.

Only in *Geococcyx, Morococcyx*, and *Coua* is M. coracobrachialis anterior a very large muscle, extending upward around the anterior edge of the humerus and to the dorsal surface of that bone. In the other genera, M. coracobrachialis anterior is a small muscle on the ventral surface of the humerus where it is closely applied to the capsule of the shoulder joint.

M. pectoralis propatagialis longus et brevis may be entirely tendinous (*Morococcyx, Dromococcyx, Tapera, Guira, Ceuthmochares, Centropus, Cuculus, Piaya*), or it may arise from M. pectoralis as a fleshy bundle (*Geococcyx, Crotophaga, Coccyzus, Saurothera, Coua, Carpococcyx, Clamator, Chrysococcyx, Surniculus, Phaenicophaeus*).

M. deltoideus minor apparently is absent only in *Coccyzus* and *Centropus*.

Three patterns in the relative development of Mm. pronator superficialis and pronator profundus are seen in the cuckoos: (1) the two muscles are about equal in length and both are relatively short—*Coccyzus, Dromococcyx, Chrysococcyx, Surniculus*; (2) they are about the same length and they extend nearly to the distal end of the radius—*Morococcyx, Guira, Centropus, Ceuth-*

mochares, Phaenicophaeus; (3) the profundus is longer than the superficialis —*Coua, Geococcyx, Crotophaga, Tapera, Piaya, Saurothera, Carpococcyx, Clamator, Cuculus.*

Cuculus and *Chrysococcyx* appear to differ from all other genera in that they possess an accessory flexor muscle of the pollex, which arises from the tendon of insertion of M. tensor patagii longus (Berger, 1955*b*: Fig. 70). In these two genera and in *Surniculus* and *Phaenicophaeus*, M. flexor digitorum profundus arises on both sides of the insertion of M. brachialis, rather than only posterior to it as in the other cuckoos.

The relative development of M. flexor carpi ulnaris brevis appears to be correlated with locomotor habits. The muscle is very short in *Geococcyx, Morococcyx, Dromococcyx, Tapera, Crotophaga, Coua, Carpococcyx, Centropus, Phaenicophaeus,* and *Ceuthmochares.* It is relatively long in *Coccyzus, Piaya, Saurothera, Guira, Clamator, Cuculus, Chrysococcyx,* and *Surniculus.*

Throughout the discussion above, I have used qualifying terms (e.g., primarily, in general, more arboreal) when referring to cuckoos as being arboreal or terrestrial. A review of the general habits and the myology of the couas may be instructive in this regard. The genus *Coua* contains a well-defined group of cuckoos that is restricted to Madagascar. Several years ago I (1953*a*: 53–54) quoted from a letter that Dr. A. L. Rand had written to me about this genus. He wrote, in part: "The three arboreal species *caerulea, cristata,* and *verreauxi* are geographical replacements. The terrestrial rain-forest species, *reynaudii* and *serriana,* have different food, one insects, one fallen fruit. In the dry forests and brush are four species, one rather wide-spread (*ruficeps*), but the other three are more restricted. *C. coquereli* and *cursor* are geographical representatives, and the much larger *C. gigas* co-exists with *C. coquereli* but overlaps the range of *C. cursor.*

"The group is, to my mind, a terrestrial type. The terrestrial species are at home, agile and graceful on the ground, swift of foot, and may prefer to escape danger on foot rather than by flying or seeking concealment. The arboreal species, and this includes *C. caerulea,* have carried over as much of this as possible into their arboreal life.

"The various modifications in range, habitat, and habits seem to be the result of an intra-group pressure and competition with little competition, in island isolation, from other groups. They have modified these without modification in structure. Thus, to use *C. caerulea* as an example of an arboreal cuckoo is a mistake. It is a terrestrial type that has taken to living in trees! Hence, its resemblance in leg proportions to *Geococcyx* is what I would expect."

Dr. Reynaud Paulian wrote (letter, January 16, 1956) that "*Coua ruficeps* walks along branches, just as the African *Musophaga* do, moving one leg

after the other in alternating movements. Only when excited will it run by a series of sharp jumps on the ground. The *Coua* walks along the ground if not afraid, but it will take to the jumping run if at all disturbed."

In view of these statements made by two men who have observed the couas in the field, it is interesting to report that I found only one difference (not correlated to size difference) in the myology of five species of *Coua*, and there is a possibility of individual variation in this feature. In *C. serriana* and *C. reynaudii*, M. extensor pollicis brevis arises by two separate heads: one from the tendon of insertion of M. extensor pollicis longus; the other, from the base of the carpometacarpus adjacent to the insertion of the tendon of M. flexor carpi ulnaris brevis. M. extensor pollicis brevis has a single head in *caerulea*, *cristata*, and *ruficeps*. The remaining wing muscles and the leg muscles exhibit an identical pattern of development in the five species. We can, indeed, agree with Dr. Rand that the couas have modified their habits without extensive modification in myology. This suggests that myological data can be used with some degree of confidence for determining closeness of relationship, providing, of course, that other factors are taken into consideration. One does not find, however, a similar uniformity in the relative lengths of the bones of the appendages within the genus *Coua*. Milne-Edwards and Grandidier (1879: 170) commented on differences in development of the leg in various species of this genus. The following is a free translation of a portion of their comments: One does not perceive any relation between the habits of the birds and the dimensions of the tarsus; thus, the tarsi are long in *Coua caerulea*, which is arboreal, and in *C. gigas* and *C. ruficeps*, which are terrestrial; they are, on the contrary, short in *C. reynaudii* and in *C. cursor*, whose habits are very different, the first being a climber, and the second a runner. The chief difference in the leg muscles of the couas is in the increased length of the tendons in the long-legged forms.

Another example of difference in habit without elaborate modification in myology may be provided by the genera *Geococcyx* and *Morococcyx*. These two presumably closely related genera exhibit essentially an identical pattern in the myology of both limbs. The well-known Roadrunner (*Geococcyx*) is a terrestrial bird that has a running speed estimated at 10 to 15 mph. *Morococcyx* also is a "Ground-Cuckoo," but little seems to be known about its life history or habits. However, Dr. Ernest P. Edwards wrote (letter, January 23, 1953) that *Morococcyx* "*walks* along branches somewhat as a dove would walk along them." Perhaps *Morococcyx*, also, is a ground-cuckoo that has taken to living in trees.

A number of other cuckoos are intermediate in locomotor habits. For example, Delacour (1947:120) characterized the species of *Phaenicophaeus*

(in which genus he included all the species of nine of Peters' genera) as being poor fliers, living among vines and bushes.

The correct interpretation of differences in myology within the family Cuculidae is complicated because some genera are parasitic and others are not. If one attempts to use myological formulae as well as breeding behavior in determining relationships among cuckoos, one is confronted with some puzzling situations, even if one excludes "E" from the muscle formulae. Among New World cuckoos, for example, *Tapera* is known to be parasitic, and the meager information available indicates that *Dromococcyx*, also, is parasitic (Giai, 1949; Neunteufel, 1951). *Tapera*, like all of the Old World parasitic cuckoos except *Eudynamis* and *Scythrops*, lacks pars iliofemoralis of the piriformis muscle, whereas *Dromococcyx*, *Eudynamis*, and *Scythrops* are, apparently, the only parasitic cuckoos that have what is traditionally considered the full cuculine muscle formula of ABXYAm. Hence, it would appear that one must discount either myological data or breeding behavior in deciding the relationships among the cuckoos. It must be emphasized, however, that we are handicapped seriously because so little is known about the life histories of the Neotropical (as well as many other) cuckoos.

Friedmann (1933) suggested that the parasitic habit is "of great antiquity" in the cuckoos and that *Tapera* developed its parasitism independently of the Old World cuckoos. I would suggest that the parasitic habit did not develop independently in *Tapera* and *Dromococcyx* but that "the ancestral Cuculine stock that reached the Americas brought with it a tendency towards parasitism (if not an actually developed parasitic habit) which has fructified in *Tapera*" (Friedmann, 1933:533) and in *Dromococcyx*. There are parasitic cuckoos in both hemispheres that possess the two basic types of cuculine muscle formulae: (1) AXYAm: Old World—*Cuculus*, *Chrysococcyx*, *Clamator*, *Surniculus*, etc.; New World—*Tapera*. (2) ABXYAm: Old World—*Eudynamis*, *Scythrops*; New World—*Dromococcyx*. Thus, if we are to place any value on morphological characters, we must assume either that parasitism has developed independently as many as four times in this one family (which seems highly unlikely) or that the parasitic habit (or tendency for it) developed in the primitive cuckoos (all ABXYAm) while still in the Old World ancestral home of the family.

Comparative Osteology

Moreau recently called attention to the considerable difference of opinion expressed by the several classifications of the touracos that have been proposed during the past 34 years. I am in no sense prepared to comment on the classification of the touracos, but I can add some pertinent remarks on the osteology of the group. Several years ago, I examined the skeletons of 14 touracos, representing four of Moreau's (1958:75) five genera and eight of his

18 species: *Corythaeola cristata*; *Crinifer piscator*; *Corythaixoides concolor* and *personata*; *Tauraco corythaix* (including *persa* and *persa buffoni*), *macrorhynchus*, and *leucotis donaldsoni*.

Verheyen (1956*a*, 1956*b*) analyzed the skeletons of touracos and cuckoos in some detail, and from this and other information taken from the literature proposed systems of classification for both the touracos and the cuckoos. With regard to the touracos, Moreau (1958:77) commented: "I understand from Verheyen (*in litt.*) that his sub-families are not based on osteological characters except for the Corytheolinae (which have 20 pre-synsacrals and five dorso-sacra, compared with nineteen and four respectively in all the other Musophagidae). The separation of *Corytheola* in this way might perhaps be justifiable, but the allocation of the remaining Musophagidae into three subfamilies can hardly be accepted."

The separation of *Corythaeola* from the other musophagids on the basis of the number of cervical or presynsacral vertebrae is not justifiable. I studied two skeletons of *Corythaeola cristata*: one had 14 cervical and 5 dorsal vertebrae, or 19 presynsacral vertebrae as in the other musophagids; the other specimen had 15 cervical and 5 dorsal vertebrae, or 20 presynsacrals, as in the single specimen examined by Verheyen. This is surely another example of individual variation in the number of cervical vertebrae within a species; in my opinion, it has no taxonomic significance. I had for study only one specimen of *Corythaixoides* (= *Gymnoschizorhis*) *personata*, but it, too, had 20 presynsacral vertebrae. Each of two specimens of *Tauraco corythaix persa* (see Moreau, 1958) had 14 cervical vertebrae, but one had 5 dorsal vertebrae, the other only 4. Hence, one specimen had the typical musophagid number of 19 presynsacral vertebrae, whereas the other had only 18. Despite these few examples of individual variation, it seems likely that the typical number of presynsacral vertebrae in the musophagids is 19: 14 cervical and 5 dorsal vertebrae.

Among the specimens studied by Verheyen, the number of free caudal vertebrae varied from 6 to 8; among my specimens, from 5 to 7.

The number of ribs that articulate directly with the sternum varies, among the several genera and within a species, from 3 to 5, with 4 being the usual number. In one specimen of *Corythaixoides concolor*, five ribs articulated with the sternum on the right side, but only four did so on the left.

If we now turn our attention to the Cuculidae, we find that the typical number of presynsacral vertebrae in most genera is 18: 14 cervical and 4 dorsal vertebrae. However, I found that each of 30 specimens of the genus *Coccyzus* had only 13 cervical and 4 dorsal vertebrae, or a total of 17 presynsacral vertebrae; one additional specimen had 14 cervical and 4 dorsal vertebrae. According to Shufeldt, *Clamator glandarius* has only 13 cervical

vertebrae; Verheyen (1956*a*:17) indicated that he examined four specimens of *C. levaillantii* and found 13 cervical vertebrae in this species; I found 13 cervical vertebrae in my single specimen of *C. jacobinus*. Apparently there are no reliable published data to indicate that any other cuculine genus has 13 cervical vertebrae. Fürbringer (1888:779), for example, is in error when he lists 13 cervical vertebrae for *Crotophaga*, except, of course, as a matter of individual variation; the genus typically has 14 cervical vertebrae. However, I found only 13 cervical and 4 dorsal vertebrae in single specimens of *Piaya* and *Saurothera*. One specimen of *Guira* had 14 cervical and 4 dorsal vertebrae, whereas a second specimen had 13 cervical and 5 dorsal vertebrae, certainly an abnormal number for cuckoos. The number of cervical and dorsal vertebrae within a genus appears to be relatively constant in the cuckoos (Berger, 1956:437), and it seems likely that the usual pattern in *Guira* is 14 cervical and 4 dorsal vertebrae. The osteology of only one genus (*Coccyzus*) can be considered to have been studied in sufficient numbers to justify much confidence in numerical data, however, so that much additional information is needed on the osteology of the cuckoos before the full significance of the data can be appreciated. Nevertheless, it is interesting to note that, apparently, *Coccyzus*, *Piaya*, *Saurothera*, and *Clamator*, each have 13 cervical vertebrae, and each genus has the same muscle formula of AEXYAm.

In my single specimen of *Carpococcyx* (United States National Museum No. 223,970), there were 15 cervical and only 3 dorsal vertebrae. There was, however, a well-developed thoracic rib (which, by definition, articulates dorsally with the synsacrum and not with a dorsal vertebra), and this rib had a direct articulation with the sternum, so that 4 ribs (3 true ribs and 1 thoracic rib) articulated with the sternum bilaterally. This represents a very unusual condition, at least among cuckoos. I suspect that it is an anomaly in this one specimen, and that *Carpococcyx*, like most other cuckoos, typically has 14 cervical and 4 dorsal vertebrae.

We may summarize some of the pertinent differences in the osteology of the two groups of birds. Touracos typically have 19 presynsacral vertebrae; most cuckoos have 18 presynsacral vertebrae, but a few have only 17. Touracos have a notched atlas; cuckoos, a perforated atlas. Touracos have a single bony canal in the hypotarsus; cuckoos have two bony canals. The sternum is double-notched in the touracos; the sternum is either single-notched or double-notched in cuckoos, sometimes (in older individuals?) it is merely fenestrate. In the touracos (all?) the clavicles are not fused ventrally to form a furcula, but the inferior ends are united by a ligament; a furcula is present in the cuckoos. As pointed out by Pycraft (1903:279) and Verheyen (1956*a*), the two dorsal processes of the coracoid are fused to form a bony canal in the touracos; the two processes do not fuse in the cuckoos. In the touracos, the

tendon of M. supracoracoideus passes through the canal in the coracoid and then through the foramen triosseum, which is bounded only by coracoid and scapula. Lowe (1943) described and illustrated differences in the structure of the ectethmoid plate and the lacrimal bone between *Tauraco* and *Cuculus*. Some cuckoos (e.g., *Centropus*) are somewhat intermediate between *Cuculus* and *Tauraco* in the development of these characters, but the over-all pattern probably is distinctive for the two families (Fig. 2).

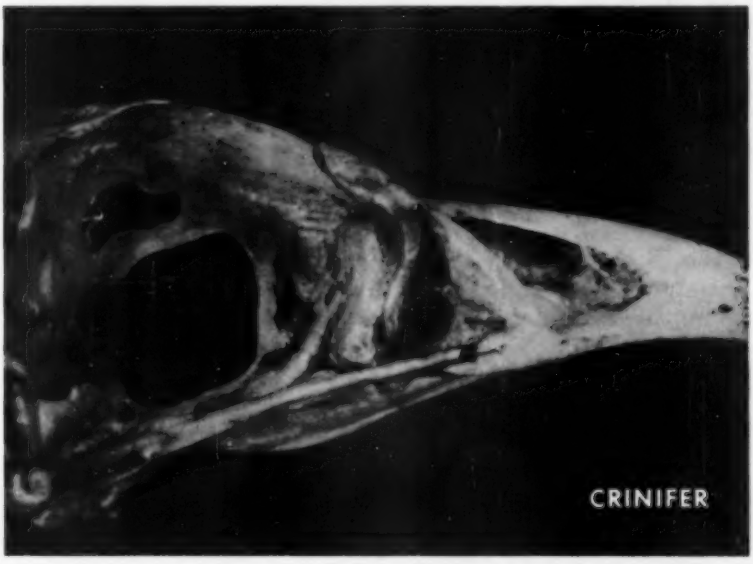

FIG. 2. Lateral view of part of skull of *Crinifer piscator* to emphasize the lacrimal bone.

COMPARATIVE PTERYLOSIS

Forbes (1885:212) remarked that the pterylosis of the Musophagidae "is peculiar, and gives no aid in determining their affinities." Nitzsch (1867: Pl. 6) illustrated the dorsal and ventral feather tracts of *Tauraco erythrolophus* ("*Musophaga paulina*"), and Lowe (1943) illustrated these tracts for *Musophaga violacea*. I found the feather tracts of *Tauraco leucotis donaldsoni* to be essentially the same as those shown in Lowe's figures.

Beddard (1885 and later) placed considerable emphasis on the value of the ventral feather tracts in determining relationships among the cuckoos, but the

entire matter is in need of a thorough re-investigation. I have pointed out elsewhere (1953*a*, 1955*b*) that two of Beddard's assumptions were wrong. It has been demonstrated, however, that there are several patterns of feather tracts among the Cuculidae. In one group (*Cuculus*, *Cacomantis*, *Surniculus*, *Ceuthmochares*, *Clamator*, *Piaya*, *Coccyzus*, *Saurothera*) there is a single ventral abdominal tract on each side. In a second group (*Chrysococcyx*, *Scythrops*, *Carpococcyx*, *Centropus*, *Eudynamis*, *Phaenicophaeus*, *Geococcyx*, *Crotophaga*, *Guira*, *Morococcyx*), the ventral abdominal tracts are paired bilaterally. Furthermore, the ventral cervical tract may bifurcate in the region of the chin (*Piaya*, *Saurothera*, *Coccyzus*, *Phaenicophaeus*), about midway down the neck (*Cuculus*, *Clamator*, *Tapera*, *Crotophaga*, *Guira*, *Carpococcyx*, *Geococcyx*, *Morococcyx*), or at the base of the neck (*Centropus*, *Ceuthmochares*, and probably *Surniculus*). Beddard (1898*b*:280) separated certain Old World cuckoos from certain New World cuckoos because the ventral cervical tract in the New World cuckoos is "double at [its] commencement." This latter group is the one for which I have stated that the ventral cervical tract bifurcates in the region of the chin. There is some minor variation in these tracts among the four genera that I have listed above, and this character is perhaps most striking in the Old World genus *Phaenicophaeus*. In *Phaenicophaeus* there are two interramal feather tracts, separated by a median apterium, and each tract is bounded laterally by a pronounced marginal apterium.

Similarly, there are differences in the pattern of the dorsal feather tracts. In *Cuculus canorus*, for example, the dorsal cervical tract is continuous with the interscapular tract, and there is a large median apterium in the latter tract (Lowe, 1943: Fig. 6). In *Coua*, *Geococcyx*, *Morococcyx*, *Carpococcyx*, *Guira*, and *Centropus*, however, the dorsal cervical tract ends abruptly at the base of the neck, and the interscapular tract begins as two independent, anteriorly-directed tracts, which fuse posteriorly to form a single median pelvic tract. There are some differences among these genera and it seems pertinent to describe both the dorsal and ventral tracts of *Carpococcyx*. I have already described these tracts in *Coua caerulea* and *C. ruficeps* (1953*b*, 1954); Shufeldt (1886) illustrated the pterylosis of *Geococcyx*; and Beddard (1885) illustrated feather tracts of *Centropus*, *Eudynamis*, *Piaya*, and *Cacomantis*. Shelford (1900) described and illustrated the pterylosis of the embryo and nestling of *Centropus sinensis*, and Hartley (in Beebe *et al.*, 1917) illustrated the feather tracts in both the embryo and adult of *Crotophaga ani*.

A median frontal apterium is wanting and the feathers of the capital feather tract are a little more sparse in *Carpococcyx radiceus* than they are in *Coua*. A large lateral apterium surrounds the orbit. The spinal cervical tract ends abruptly at the junction of the neck and thorax, and there is a relatively wide

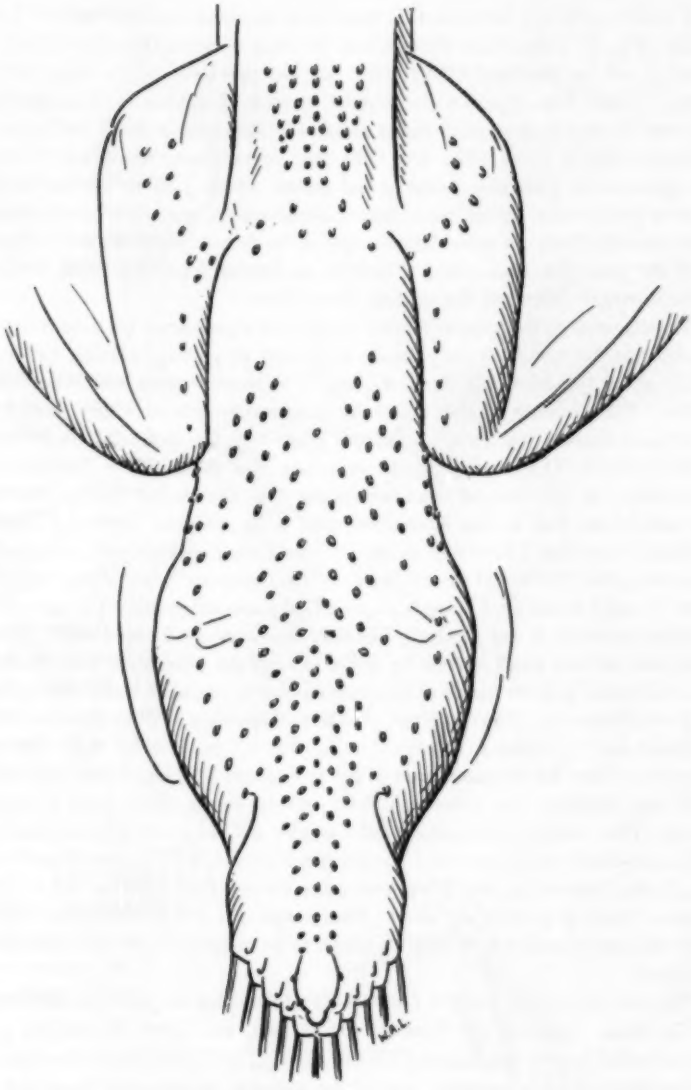

FIG. 3. Dorsal feather tracts of *Carpococcyx radiceus*.

(20 mm.) apterium between this tract and the interscapular tracts. These tracts (Fig. 3) differ from those found in other cuckoos thus far studied, as pointed out by Beddard (1901:201) but not precisely in the way that he stated. There does appear to be a short, narrow, V-shaped median apterium between the two interscapular tracts anteriorly, although in shape and extent it is unlike that in *Coua* (Fig. 4). The two interscapular tracts are continuous posteriorly with the dorsal spinal tracts, which join to form a single, median pelvic tract. In addition, lateral dorsal tracts, essentially single-rowed, pass caudally from the anterolateral edge of the dorsal spinal tracts to the area over the posterior iliac crests. There is an almost featherless area between these bilateral tracts and the median pelvic tract.

Turning now to the ventral feather tracts of *Carpococcyx*, we note first that the marginal apteria are very small, if present at all (an incision had been made along the mandible, thus making this determination somewhat unreliable). The presence or absence of the marginal apteria on either side of the interramal feather tract was one of the diagnostic features used by Beddard (1898*b*:281): (1) ventral tract occupying the entire space between the mandibles; or (2) ventral tract occupying only the median region between the mandibles, that is, the interramal tract is bounded by marginal apteria. Judging from what I have seen to date, I would say that Beddard's criteria for separating the Old World *Centropus* (= "*Pyrrhocentor*") and *Coua* from the New World *Geococcyx*, *Crotophaga*, and *Guira* are untenable. The pattern in *Cuculus* certainly is not precisely like that illustrated by Lowe (1943) in that there are definite small apteria on either side of the interramal tract; nor, in this character, is there such a close similarity between *Cuculus* and *Musophaga* as Lowe illustrated. The marginal apteria in *Centropus* are like those in *Coua caerulea* and *C. ruficeps*. It seems to me that we are dealing here with the degree to which the marginal apteria are developed. The narrowest interramal tract, and therefore the widest marginal apteria, seems to be found in *Crotophaga*. Thus between *Crotophaga* and *Cuculus* or *Centropus* there is a marked difference in the development of the marginal apteria, but *Tapera* (Figs. 5 and 6), *Guira*, *Geococcyx*, and *Morococcyx* are intermediate between the two extremes. And, as pointed out above, *Phaenicophaeus* and certain other genera have two interramal tracts, each of which is bounded laterally by a marginal apterium.

The ventral cervical tract of *Carpococcyx* bifurcates at about the midlength of the neck. Opposite the head of the furcula, two rows of feathers pass dorsocaudad to join the humeral feather tract. The ventral tract bifurcates at about the level of the anterior end of the sternum, forming an inner and an outer ventral abdominal tract bilaterally. The inner tract is composed of a double row of feathers anteriorly, but of a single row in the posterior half of

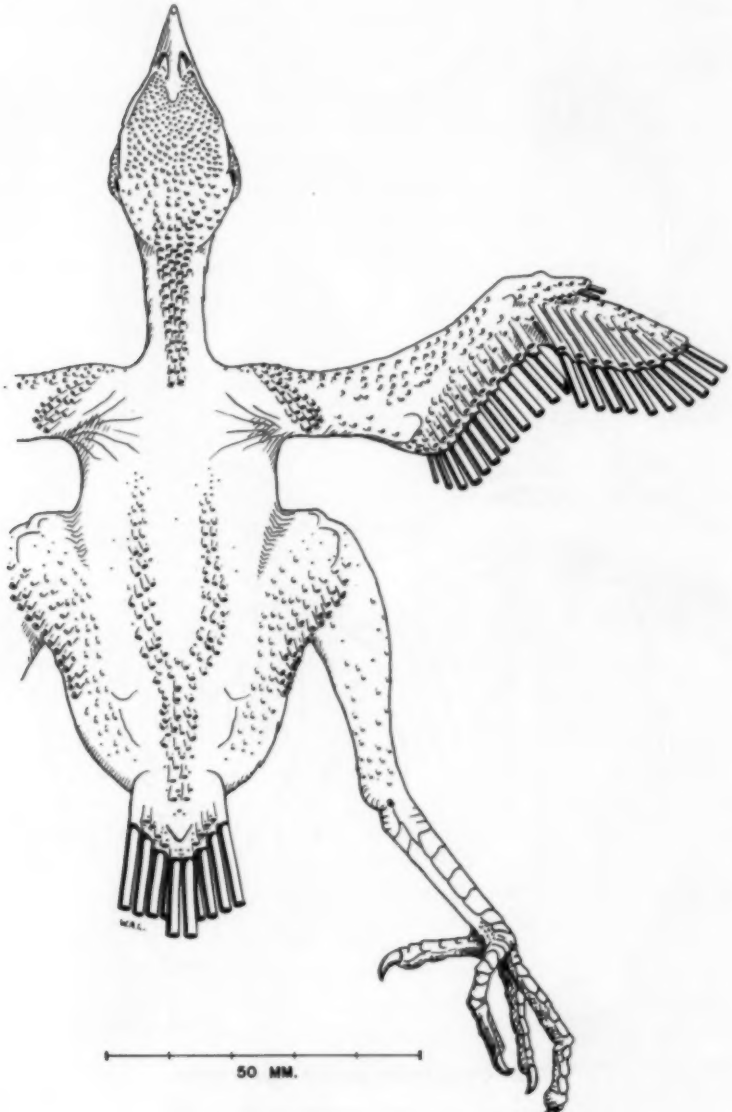

FIG. 4. Dorsal feather tracts of nestling *Coua ruficeps*.

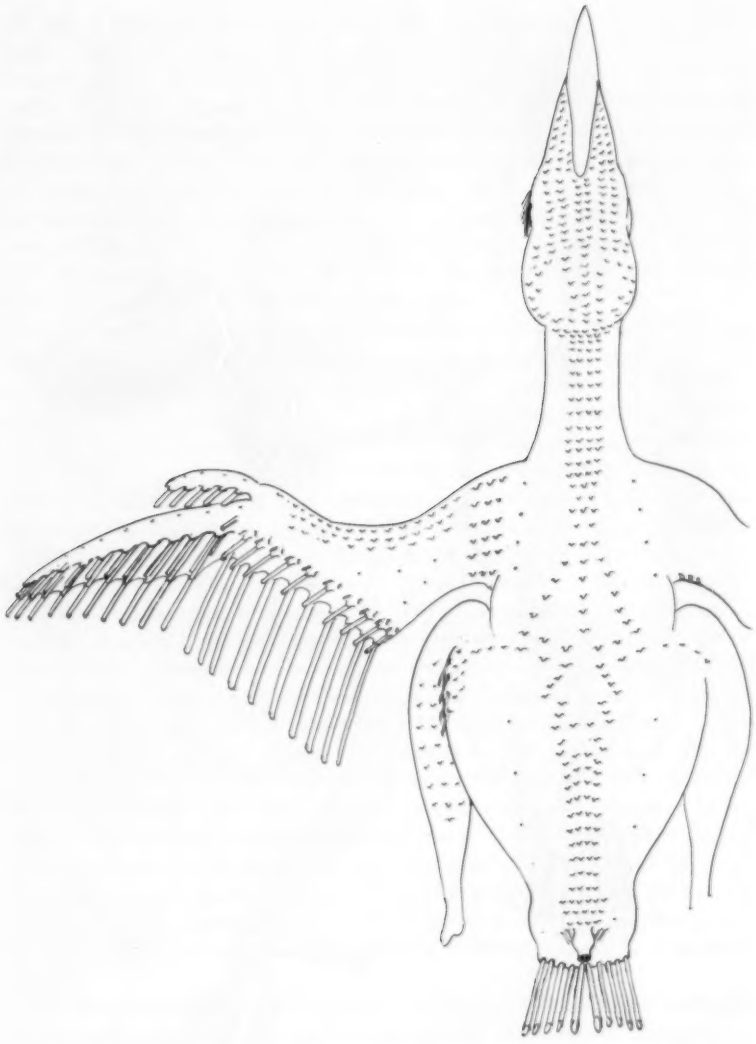

FIG. 5. Dorsal feather tracts of *Tapera naevia*.

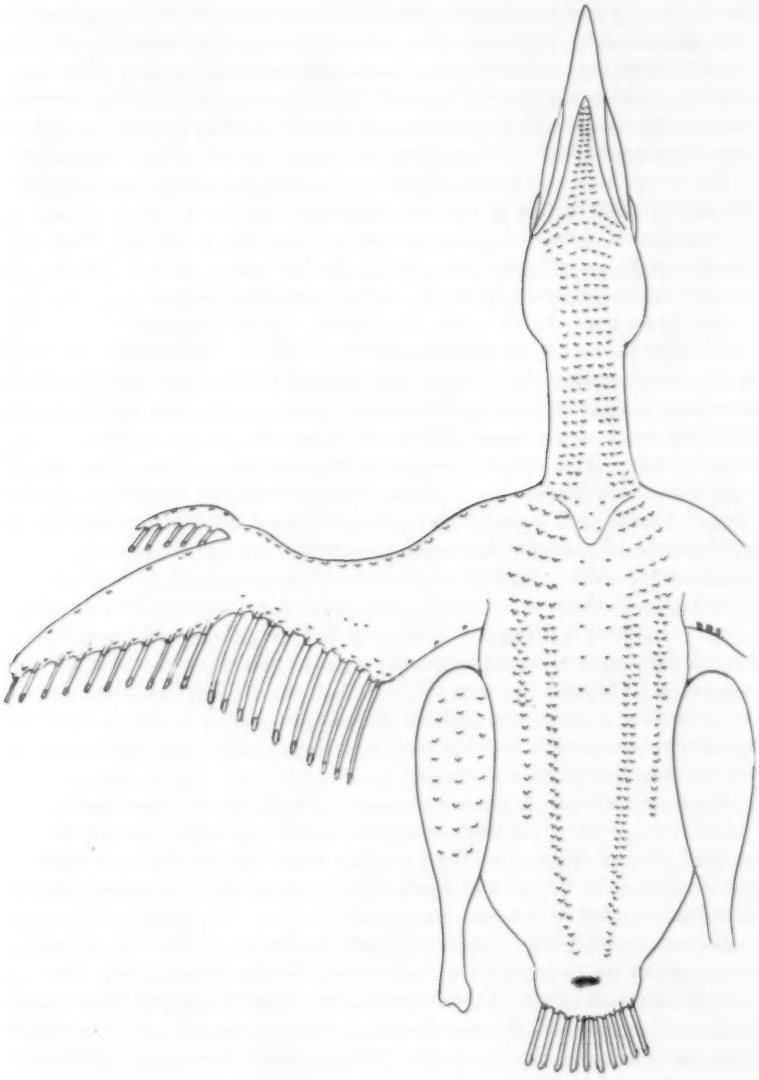

FIG. 6. Ventral feather tracts of *Tapera naevia*.

its extent; this tract terminates a short distance (about 6 mm.) in front, and a little anterolateral, of the vent. The outer abdominal tract anteriorly is composed of three rows of four feathers each, but throughout most of its extent it is composed of a single row of feathers. This row ends about midway between the posterior margin of the sternum and the vent; it does not turn inward to meet the inner abdominal tract. From the lateral margin of the anterior part of the outer abdominal tract, a single row of feathers passes dorsolaterad to the posteoventral surface of the arm (humerus).

There are 10 primaries in *Carpococcyx*. The wing is eutaxic. There are apparently 11 secondaries; the outer eight have large quills, whereas the inner three are progressively smaller and are more like coverts in size, but they are in direct line with the outer secondaries. Beddard considered only the distal eight feathers to be secondaries. There are five alula quills; the molt was in progress when the specimen was collected so that it was not possible to determine the relative lengths of the alula feathers. A relatively well-developed (40 mm. long) carpal remex was found bilaterally, but no evidence of the carpal covert. There are 10 rectrices and 10 upper tail coverts. The femoral tract laterally is developed as in *Coua ruficeps*; medially, the thigh is almost devoid of feathers. The crural tract is best developed anteriorly, where there is a triple row of feathers proximally (somewhat irregular in pattern) and a single row distally; there are three rows of widely-spaced feathers on the lateral side of the crus; medially, there are a few scattered feathers; and posteriorly, there is a single row of small feathers. The crural tracts do not extend downward on to the tarsometatarsus, as they do in *Cuculus*, *Chrysococcyx*, and *Clamator*. Sharpe (1873:579) spoke of *Cuculus*, *Chrysococcyx*, and *Clamator* as having "accipitrine thigh-feathers," and he reported that the rim around the external naris is swollen in these genera; *Surniculus lugubris* also exhibits both of these characters.

Apparently all cuckoos have 10 primaries. Most cuckoos have either 9 or 10 secondaries; *Scythrops* is said to have 13; *Carpococcyx* and *Centropus* appear to have 11; and the nestling *Coua ruficeps* seems to have 12 (see, however, the discussion by Berger and Lunk, 1954). *Guira* and *Crotophaga* have 8 rectrices; all other cuckoos are said to have 10.

Despite the variation in pattern of both the dorsal and the ventral feather tracts among the cuckoos, no cuckoo yet studied has feather tracts (particularly dorsally) like those of the touracos. The oil gland is tufted in touracos; it is nude in cuckoos. An aftershaft is present in touracos; it is absent or vestigial in cuckoos (Miller, 1924). Well-developed "eyelashes" are characteristic of cuckoos. The eyelashes may be featherlike, as in *Cuculus*, *Chrysococcyx*, *Clamator*, and *Surniculus*, or they may be "hairlike," as in *Coua*, *Geococcyx*, *Morococcyx*, *Dromococcyx*, *Tapera*, *Guira*, *Crotophaga*, *Piaya*,

Saurothera, *Ceuthmochares*, *Centropus*, and *Phaenicophaeus*. The small, black, hairlike eyelashes are least conspicuous in *Phaenicophaeus pyrrhocephalus*; those of *Dasylophus* (= *Phaenicophaeus*?) *superciliosus* are said to be large and scarlet. Eyelashes are absent in *Tauraco leucotis donaldsoni*, and both eyelids are covered by fleshy caruncles which are especially prominent dorsal to the upper eyelid. There appear to be seven alula quills attached to the pollex in *Tauraco*; these increase in length from proximal to distal: No. 1 is 23 mm. long; No. 2, 28 mm.; No. 3, 33 mm.; No. 4, 36 mm.; No. 5, 44 mm.; No. 6, 50 mm; No. 7, 52 mm. Cuckoos apparently have either four or five alula quills. The innermost, the outermost, or one of the intermediate feathers may be the longest in the series.

The Cuculine Syrinx

There are few anatomical structures throughout the families of birds that need study as badly as the syrinx. Except for a very few isolated instances, our knowledge of both the passerine and the nonpasserine syrinx is based largely on work published during the last century (e.g., Müller, 1878). Such pioneers as Müller, Garrod, Forbes, Fürbringer, and Gadow were remarkably astute scholars of the old school and any thorough anatomical study must begin with a careful analysis of their papers. Nevertheless, the work of the past needs to be corroborated and extended, using both gross and microscopic techniques. We need detailed comparative studies of the syrinx interpreted in terms of modern concepts of anatomy and of systematics. For such studies, one needs a number of specimens of each species in order to work out all relationships carefully. The intrinsic syringeal muscles usually are very small and they often are poorly preserved in alcoholic specimens. In addition to gross descriptions, microscopic analyses and embryological studies of developmental stages of the syrinx *in both sexes* would undoubtedly add much to our understanding of the significance of the adult configuration of the syrinx and its relation to muscles and to the tracheobronchial tree.

I can do little more here than verify statements in the literature and summarize present knowledge of the cuculine syrinx. The following cuckoos are known to have a bronchial syrinx: *Centropus*, *Carpococcyx*, *Coua*, *Geococcyx*, *Morococcyx*, *Dromococcyx*, *Crotophaga*, and *Guira*. Within this group, however, there is a considerable difference as to the location of the syrinx within the bronchi, as pointed out by Beddard (1885:170–174). Beddard reported (1901:202) that "the syrinx of *Carpococcyx* . . . is the most purely bronchial syrinx that exists among the Cuculidae; it is even more exaggerated than that of *Crotophaga*," and he added that the syringes of *Centropus* and *Geococcyx* "present us with an intermediate stage between the typical tracheo-bronchial syrinx of the Phoenicophainae and the extraordinarily specialized bronchial

syrinx of *Crotophaga* and of *Carpococcyx*." The syrinx of *Centropus superciliosus* (Fig. 11), however, approaches the "exaggerated" condition found in *Carpococcyx* (Beddard, 1901:203), and it appears to be different from the syrinx of *Centropus ateralbus* (Beddard, 1885:172). This suggests that a comparative study of the syrinx among the many species of *Centropus* would be a fruitful project.

All other cuckoos studied, including *Tapera*, have a tracheobronchial syrinx. Beddard remarked (1902:605–606) that the syrinx of *Rhamphococcyx* (= *Phaenicophaeus* according to some writers) exhibits "a hint of a development into the bronchial syrinx of the Centropine Cuckoos." Hence, as with other anatomical information, we seem to know just enough about the anatomy of the cuculine syrinx to suggest many intriguing problems for further study and not enough to understand completely the significance of the data that are available. My material was not suitable for microscopic study, and I present here figures (Figs. 7–11) illustrating the gross differences in the syrinx of one series of cuckoos. A knowledge of the finer structure of the cuculine syrinx would undoubtedly be instructive. It should be noted that M. sternotrachealis inserts very near the tracheal bifurcation in *Centropus*, whereas it inserts some distance from the bifurcation in the other genera. Only in the syrinx of *Crotophaga* (a female) did I find two pairs of intrinsic syringeal muscles; there is a single pair of intrinsic muscles in the other genera.

Discussion

There has been a tendency by some contemporary writers to state flatly that certain anatomical features in birds are so stable in an evolutionary sense that similarities in these characters "prove" relationship among the birds concerned. One may make such a basic assumption about a single character and then proceed to "prove" all sorts of inter-relationships that then permit the construction of an elaborate phylogenetic tree, which the author may state or imply is to be accepted without qualification or question. Most often such authors base their conclusions on a smattering of information about a particular anatomical character. When, for example, an author purports to "explain" the course of evolution in all oscine passeriform birds on the basis of a single bone of the skull and on the size of the birds, I believe that we have reached the ultimate in this type of systematic approach, one which might aptly be termed "the pseudo-anatomical approach." Other examples could be cited. The naive confidence in, and the exaggerated positive interpretation of, inadequate data expressed by such authors does a great disservice to anatomical studies and to the application of anatomical information to avian taxonomy.

I doubt that we know enough about avian anatomy or about the interrelationships between structure and function—and all of the related problems

FIG. 7

FIG. 8

FIG. 10

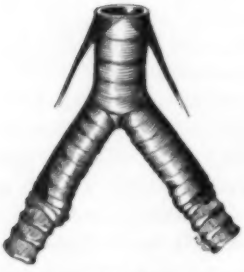

FIG. 9

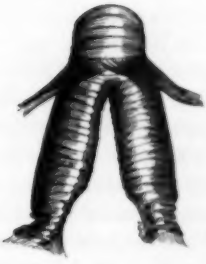

FIG. 11

FIG. 7. Tracheobronchial syrinx of *Piaya cayana.*
FIG. 8. Bronchial syrinx of *Guira guira.*
FIG. 9. Bronchial syrinx of *Morococcyx erythropygus.*
FIG. 10. Bronchial syrinx of *Crotophaga sulcirostris.*
FIG. 11. Bronchial syrinx of *Centropus superciliosus.*

of convergence and divergence among birds—to justify such confidence. Miller (1937:58–59), Rinker, and others have discussed this problem and that of the inequality of values to be assigned to anatomical features in the study of both birds and mammals. Thus, Rinker (1954:117), in speaking of rodents, wrote: "Even the segregation of characters into adaptive and nonadaptive categories, or a classification based on current survival value, is, in my opinion, a highly subjective approach. I do not believe that the present state of knowledge will allow this approach to be used with any appreciable degree of certainty. It appears to me that success in such an attempt would require much greater insight into the relationships of structure and function, into the basis of habitat preferences (or restrictions), and into many more phenomena than is possible at present." It does not seem to me to be an exaggeration to make a similar statement about birds, particularly when it seems that we know less about the significance of anatomical characters in birds than in mammals. Moreover, we can agree wholeheartedly with Enlow and Brown (1958:221) when they caution: "The projection of preconceived concepts and prejudices of evolutionary mechanics into the interpretation of observations is a consideration that must consciously, and continually, be recognized and evaluated. It is a constant temptation to look for, and thereby find, a logical, uni-linear assemblage of structural changes that conform with and confirm some preexisting idea on how things should be happening."

Before summarizing the data presented in this paper, it will be instructive to consider Peters' (1940) classification of the cuckoos. There seems to be general agreement that Peters' classification is unsatisfactory. He had little published information on cuculine anatomy to rely on, and I suspect that his system was based primarily on two factors: parasitism and geographical distribution. An analysis of his subfamilies will give further insight into some of the problems involved and will reveal where further work is needed.

Peters' subfamily Cuculinae is composed of Old World cuckoos that have parasitic breeding habits. For most of the included genera the muscle formula is AXYAm, but for *Eudynamis* and *Scythrops* it is ABXYAm. *Clamator* has 13 cervical vertebrae; so far as is known, the other genera have 14. There is a single ventral abdominal feather tract on each side in *Cuculus*, *Cacomantis*, *Clamator*, and *Surniculus*; these tracts are paired bilaterally in *Chrysococcyx*, *Scythrops*, and *Eudynamis*. Baker (1927) erected the subfamily Eudynaminae for the single genus *Eudynamis*.

An analysis of Peters' subfamily Phaenicophaeinae—which he admitted was a "catch-all" group—is even more interesting. He included in this subfamily three nonparasitic American genera and nine nonparasitic Old World genera. Each of the American genera (*Coccyzus*, *Piaya*, *Saurothera*) has a muscle formula of AEXYAm, a single ventral abdominal feather tract bilaterally, and,

apparently, 13 cervical vertebrae. Six of the nine Old World genera are known to have the muscle formula of ABXYAm. Of the two genera studied for this paper, *Ceuthmochares* has a single ventral abdominal feather tract bilaterally, whereas *Phaenicophaeus* has paired tracts bilaterally. Both genera have 14 cervical vertebrae and a muscle formula of ABEXYAm. It should be pointed out that Delacour and Mayr (1945) did not recognize eight of the nine Old World genera (including *Ceuthmochares*) listed by Peters, and, therefore, placed all of the species in the genus *Phaenicophaeus*. Bannerman (1933), on the other hand, placed *Ceuthmochares* in his subfamily Centropodinae.

The Crotophaginae (*Crotophaga* and *Guira*) are New World cuckoos that have eight rectrices, a muscle formula of ABEXYAm, and social nesting habits.

Peters' subfamily Neomorphinae contains one Old World genus (*Carpococcyx*) and five New World genera. All except *Tapera* (AXYAm) have a muscle formula of ABXYAm. *Tapera* and *Dromococcyx* are parasitic; so far as is known, the other genera are not parasitic, although Makatsch (1955:34) suggested that *Neomorphus* might have parasitic nesting habits (but see, Sick, 1949). Shelley (1891:423) placed *Tapera* (= "*Diplopterus*") and *Dromococcyx* in the subfamily Diplopterinae (= Taperinae), whereas Gadow and Selenka (1893:214) put *Tapera* in their subfamily Cuculinae (parasitic, AXYAm, syrinx tracheobronchial).

The subfamily Couinae presumably was established because the single genus is restricted to Madagascar. There is little in the internal anatomy to separate *Coua* from *Geococcyx* or *Morococcyx*.

Peters' last subfamily, the Centropodinae, contains the single Old World genus *Centropus* with some 27 species and 55 subspecies. These are widespread (from Australia, the Philippines, and China to Africa and Madagascar), nonparasitic cuckoos that have a very long, straight and sharp claw on the hallux (of many, but not all, of the species), thus the name of Lark-heeled Cuckoos. The coucals build a bulky globular nest that has a side entrance (Delacour, 1947; Loke, 1953), but I suspect that most authors have erected the subfamily primarily on the basis of the long claw on the hallux.

Both Beddard (1898*b*) and Pycraft (1903) adopted several anatomical features—leg-muscle formulae, patterns of the feather tracts, skeletal characters, and the structure of the syrinx—in an attempt to determine cuculine relationships, but, as in the present paper, each author had information from less than half of all the genera. Beddard placed primary emphasis on the syrinx and the leg-muscle formulae (and omitted skeletal characters) in assigning cuckoos to three subfamilies. Pycraft omitted consideration of feather tracts and used skeletal characters (sternum and pectineal process)

and the syrinx in arranging the genera. The divergence in the placement of genera between these two systems was considerable.

The difficulty of deciding relationships among the genera of cuckoos seems to result largely from the fact that anatomical characters often presumed to be very stable in an evolutionary sense exhibit several patterns among the cuckoos. Thus, the muscle formula may be AXYAm or ABXYAm; the syrinx may be bronchial or tracheobronchial; the sternum may be single-notched or double-notched; there may or may not be an apterium between the dorsal cervical and the interscapular feather tracts; and the ventral abdominal feather tracts may be either single or double bilaterally. Similarly, parasitic breeding habits have developed in genera possessing both types of muscle formula, both types of syrinx, both types of sternum, both types of ventral feather tracts, and, perhaps, both types of dorsal feather pattern. Moreover, genera with a bronchial or a tracheobronchial syrinx, those with a single-notched or a double-notched sternum, etc., are found in both the Old World and the New World. These points may be illustrated by constructing a key using such anatomical features rather than using only parasitic breeding habits, geographical distribution, or the appearance of the study skin as a basis for classification. It is obvious that an author can focus the reader's attention on certain relationships by the relative weight placed on anatomical characters in constructing such keys. To demonstrate this point, I present three different keys (Tables 1–3), which embody anatomical features used by Beddard and Pycraft, as well as other features discussed in this paper; by using information reported by Beddard, I have added a few genera not examined for this paper. It is obvious, also, that the data in the tables can be arranged in several other ways.

If we consider only Table 1 for the moment, we can say, in addition, that the genera in Group I have a well-developed peroneus longus muscle; the genera in Group II, except for *Tapera*, have a weakly-developed peroneus longus muscle. M. iliacus ("E") is absent in the Old World genera of Group I. All the genera in Group I have a bronchial syrinx, bilaterally paired ventral abdominal feather tracts, and 14 cervical vertebrae; most of the genera are nonparasitic, but two have developed social nesting habits. Sick (1953*a*, 1953*b*) reported that *Tapera* and *Dromococcyx* are similar in certain external features and in general habits, but the two genera are unlike in internal characters. One would conclude that the superficial similarities in appearance are the result of convergence.

I mentioned above (p. 90) that four genera (*Cuculus*, *Chrysococcyx*, *Clamator*, and *Surniculus*) have "accipitrine" thigh feathers and raised narial rims, but these genera differ considerably in other morphological features. All four genera have parasitic nesting habits.

After examining the tables, one can see why it would be much easier to classify the cuckoos on the basis of breeding habits or on geographical distribution rather than on the basis of internal anatomical characters.

Still other anatomical features of the cuckoos need to be studied: the morphology of the head, particularly the jaw muscles and nerves (see, for example, Barnikol, 1953, and Starck, 1959); a comparative study of the viscera, the vascular system, and the brachial and lumbosacral plexuses.

Summary

As a result of this introduction to an anatomical study of cuckoos and touracos, I agree with those who have proposed that the touracos (Musophagidae) deserve ordinal rank, the Musophagiformes. Table 4 presents comparative data on the cuckoos and on *Tauraco leucotis donaldsoni*. Because they are present in all genera studied for this paper, I have not placed emphasis on two muscles that I recently (1959) proposed be added to muscle formulae: "F," M. plantaris; "G," M. popliteus. They are included in Table 4.

The following wing muscles are absent in *Tauraco leucotis donaldsoni*: cucullaris, pars propatagialis; biceps slip; anconaeus coracoideus; entepicondyloulnaris; flexor metacarpi brevis. The following leg muscles are absent in *Tauraco*: iliotrochantericus medius ("C"); iliacus ("E"); extensor brevis digiti III; adductor digiti II; adductor digiti IV.

The relatively large assemblage of zygodactyl birds that have been grouped together as cuckoos contains genera exhibiting a considerable diversity in internal morphology. It is an old group, first reported from the Oligocene Epoch. One might speculate that the ancestral cuckoos had a more complete complex of thigh muscles than do the modern forms, that they had a tracheobronchial syrinx, and that they had a propensity for developing parasitic nesting habits. Two lines of specialization might then be proposed. One group, with primarily terrestrial habits, tended to retain the thigh muscles but developed a bronchial syrinx. The other, more arboreal, group retained the tracheobronchial syrinx, tended to lose certain thigh muscles, and tended to develop parasitic breeding habits. However, there seems to be little correlation between the type of sternum and the other anatomical characters studied. Some of the cursorial genera (e.g., *Geococcyx*) have a double-notched sternum, whereas others (e.g., *Carpococcyx*) have a single-notched sternum. Similarly, both types of sternum are found among the more arboreal cuckoos. In view of the presumed occurrence of the bronchial type of syrinx in some, but not all, owls (as well as in a few other birds), one might question the significance of the bronchial syrinx, especially because of the several patterns found among the cuckoos.

Data presented in this paper reveal some of the pitfalls encountered when

TABLE 1

ANATOMICAL RELATIONS OF CUCKOOS

Group I. Bronchial syrinx; ABE(±)XYAm; ventral abdominal feather tracts double bilaterally; 14 cervical vertebrae.
1. Sternum double-notched; dorsal cervical and interscapular feather tracts separated by an apterium; M. flexor hallucis longus inserts on hallux.
a. M. flexor metacarpi brevis absent: *Coua* (E absent), *Geococcyx*, *Morococcyx*, *Neomorphus*?
b. M. flexor metacarpi brevis present; parasitic; E?; dorsal feather tracts?: *Dromococcyx*
2. Sternum single-notched
a. M. flexor hallucis longus inserts on hallux
1) dorsal cervical tract is continuous with interscapular tract; social nesting habits: *Crotophaga*
2) dorsal cervical tract separated from interscapular tract by an apterium
a) M. flexor metacarpi brevis present; social nesting habits: *Guira*
b) M. flexor metacarpi brevis absent; E absent; nonparasitic: *Carpococcyx*
b. M. flexor hallucis longus does not insert on hallux; E absent; nonparasitic: *Centropus*

Group II. Tracheobronchial syrinx; dorsal cervical feather tract is continuous with interscapular tract.
1. ABE(±?)XYAm
a. Sternum double-notched; nonparasitic; E present.
1) ventral abdominal tracts double bilaterally: *Phaenicophaeus*
2) ventral abdominal tracts single bilaterally: *Ceuthmochares*
b. Sternum single-notched; parasitic; ventral abdominal feather tracts double bilaterally (from Beddard): *Scythrops*, *Eudynamis*
2. AEXYAm; sternum double-notched; ventral abdominal tracts single.
a. 14 cervical vertebrae; parasitic: *Tapera*, *Surniculus*
b. 13 cervical vertebrae
1) parasitic: *Clamator*
2) nonparasitic: *Coccyzus*, *Saurothera*, *Piaya*
3. AXYAm; parasitic
a. Sternum double-notched; ventral abdominal tracts double: *Chrysococcyx*
b. Sternum single-notched; ventral abdominal tracts single: *Cuculus*, *Pachycoccyx*

TABLE 2

ANATOMICAL RELATIONS OF CUCKOOS

Group I. ABXYAm.	
1. Bronchial syrinx; ventral abdominal feather tracts double; 14 cervical vertebrae.	
a. Dorsal cervical and interscapular feather tracts are separated by an apterium.	
1) M. flexor hallucis longus does not insert on hallux; sternum single-notched; M. flexor metacarpi brevis present; nonparasitic:	*Centropus*
2) M. flexor hallucis longus inserts on hallux.	
a) Sternum double-notched	
1—M. flexor metacarpi brevis absent; nonparasitic:	*Coua, Geococcyx, Morococcyx, Neomorphus?*
2—M. flexor metacarpi brevis present; parasitic; dorsal feather tracts ?:	*Dromococcyx*
b) Sternum single-notched	
1—M. flexor metacarpi brevis absent; nonparasitic:	*Carpococcyx*
2—M. flexor metacarpi brevis present; social nesting habits:	*Guira*
b. Dorsal cervical tract continuous with interscapular feather tract; sternum single-notched; social nesting habits:	*Crotophaga*
2. Tracheobronchial syrinx; dorsal cervical tract is continuous with interscapular feather tract.	
a. Sternum single-notched; parasitic; ventral abdominal feather tracts double:	*Scythrops, Eudynamis*
b. Sternum double-notched; nonparasitic	
1) ventral abdominal tracts double:	*Phaenicophaeus*
2) ventral abdominal tracts single:	*Ceuthmochares*
Group II. AXYAm; tracheobronchial syrinx; dorsal cervical tract continuous with interscapular feather tract.	
1. Sternum double-notched	
a. Ventral abdominal tracts single bilaterally	
1) 14 cervical vertebrae; parasitic:	*Tapera, Surniculus*
2) 13 cervical vertebrae	
a) nonparasitic:	*Coccyzus, Saurothera, Piaya*
b) parasitic:	*Clamator*
b. Ventral abdominal tracts double; parasitic:	*Chrysococcyx*
2. Sternum single-notched; ventral abdominal tracts single; parasitic:	*Cuculus*

TABLE 3

ANATOMICAL RELATIONS OF CUCKOOS

Group I. Sternum double-notched.	
1. Bronchial syrinx; ABE(±)XYAm	
a. M. flexor metacarpi brevis absent; nonparasitic:	*Coua, Geococcyx, Morococcyx, Neomorphus?*
b. M. flexor metacarpi brevis present; parasitic:	*Dromococcyx*
2. Tracheobronchial syrinx	
a. ABEXYAm; nonparasitic	
1) Ventral abdominal tracts double:	*Phaenicophaeus*
2) Ventral abdominal tracts single:	*Ceuthmochares*
b. AEXYAm; ventral abdominal tracts single	
1) 14 cervical vertebrae; parasitic:	*Tapera, Surniculus*
2) 13 cervical vertebrae	
a) parasitic:	*Clamator*
b) nonparasitic:	*Coccyzus, Saurothera, Piaya*
c. AXYAm; ventral tracts double; parasitic:	*Chrysococcyx*
Group II. Sternum single-notched.	
1. Bronchial syrinx	
a. M. flexor hallucis longus inserts on hallux	
1) Dorsal cervical tract continuous with interscapular tract; social nesting habits:	*Crotophaga*
2) Dorsal cervical tract separated from interscapular tract by an apterium.	
a) Flexor metacarpi brevis present; social nesting habits:	*Guira*
b) M. flexor metacarpi brevis absent; E absent; nonparasitic:	*Carpococcyx*
b. M. flexor hallucis longus does not insert on hallux; E. absent; nonparasitic:	*Centropus*
2. Tracheobronchial syrinx; parasitic	
a. ABXYAm; ventral abdominal tracts double:	*Scythrops, Eudynamis*
b. AXYAm; ventral abdominal tracts single:	*Cuculus, Pachycoccyx*

one compares only a few anatomical characters in single representatives of two or more families of birds. To illustrate that it is unwise to draw broad conclusions on relationships after dissecting only one or two representatives of each of several families, we may cite as examples the relative development of M. iliotibialis in *Tauraco* and in *Cuculus* and the intergeneric differences in relative development of M. peroneus longus or M. pronator superficialis and M. pronator profundus among the cuckoos.

TABLE 4

ANATOMICAL CHARACTERS OF CUCKOOS AND TOURACOS

Cuculidae	Tauraco leucotis
1. AFGXYAm, AEFGXYAm, ABFGXY Am, ABEFGXYAm	1. ABDFGXYAmV
2. Expansor secundariorum is cuculine	2. Expansor secundariorum is ciconine
3. 2 bony canals in hypotarsus	3. 1 bony canal in hypotarsus
4. 17 or 18 presynsacral vertebrae; 4 dorsal vertebrae typical	4. 19 presynsacral vertebrae; 5 dorsal vertebrae typical
5. Perforated atlas	5. Notched atlas
6. Typical furcula present	6. Furcula absent
7. No bony canal formed by coracoid	7. Bony canal is formed by the dorsal processes of the coracoid
8. Lacrimal bone is "cuculine"	8. Lacrimal bone is "musophagine"
9. Oil gland is nude	9. Oil gland is tufted
10. Aftershaft is absent or vestigial	10. Aftershaft is present
11. Eyelashes are characteristic	11. Eyelashes are absent
12. Pattern of dorsal feather tracts is dissimilar	

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UNIVERSITY OF MICHIGAN MEDICAL SCHOOL, ANN ARBOR, MICHIGAN, MAY 9, 1959

NEW LIFE MEMBER

James M. Hartshorne is a graduate student at Cornell University undertaking a doctoral research program involving a study of the development of vocalization in the Eastern Bluebird. Also, he has studied zoology at the University of Lausanne, Switzerland, and has received his MS degree from Cornell. His interest in bird vocalizations has not confined him to the study of his hand-raised bluebirds in their special sound isolation chambers in a laboratory. He has also made voice recordings in the field under various conditions, for example (as the photograph shows), of Trumpeter Swans at Red Rock Lakes Refuge, Montana, in March when the area was still completely snowbound. The snow plane shown in the photograph was a necessary addition to his recording equipment. Mr. Hartshorne, in addition to being married and the father of two boys and a girl, is a ham radio operator, a photographer, and a member of the A. O. U., the Cooper Ornithological Society, B. O. U., Ecological Society of America, etc.

GENERAL NOTES

Red-crowned Ant-Tanagers, Tawny-crowned Greenlets, and forest flocks.—While studying Red-crowned and Red-throated Ant-Tanagers (*Habia rubica and H. gutturalis*) in 1957 at Gallon Jug, British Honduras, I took occasional notes on their association with the flocks of small insectivorous birds that, like the chickadee-titmouse flocks of the United States, wander through the forest searching for their randomly dispersed food. Red-crowned Ant-Tanagers were more often members of the wandering flocks than were Red-throated Ant-Tanagers, partly because the latter species spent much time with the birds that followed army ants.

The following list gives the most frequent companions of *H. rubica* in the flocks from March 3 to July 1 (except as noted); it is abbreviated from a list of 67 species in a thesis (1958. "The Foraging Behavior of Ant-Tanagers in British Honduras") in the Louisiana State University Library. Each record represents a period of five minutes or more when a species foraged alongside ant-tanagers.

Species	Records	Individuals
Hylophilus ochraceiceps	166	322
Xiphorhynchus flavigaster	58	69
Xenops minutus	42	54
Myiobius sulphureipygius	41	41
Microrhopias quixensis	38	89
Ramphocaenus rufiventris	37	44
Henicorhina leucosticta	36	63
Thryothorus maculipectus	33	41
Helmitheros vermivorus (to April 10)	22	23
Sittasomus griseicapillus	22	22
Mniotilta varia (to April 15)	21	22
Oncostoma cinereigulare	20	22

Tawny-crowned Greenlets (*Hylophilus ochraceiceps*) were so often companions of ant-tanagers that I learned, when the latter stopped calling and consequently became very difficult to follow, to listen for the plaintive calls of the greenlets. Several of the above 166 records represent one to three hours of continuous association between the two species. On several occasions when ant-tanagers darted off to a territorial dispute the greenlets that had been accompanying them called *d'd'd'dzee-errr* and *jwai jwai jwai* rapidly, flitted their wings, and darted rapidly around. The greenlets looked everywhere until apparently the distant song of the ant-tanager dispute became audible, when they hurried off toward the commotion. Often while two male ant-tanagers warbled and chattered during a territorial dispute the lisping, nasal notes of a greenlet territorial dispute came from the nearby undergrowth. Frequently the greenlets foraged high when the ant-tanagers foraged high, and descended when the ant-tanagers did. The two species occasionally bathed and preened together, too.

Though the wandering flocks were largest in late February and late July, they were larger and more frequent during the intervening main nesting period than are chickadee-titmouse flocks of northern latitudes during nesting. Several factors might cause such a difference. Many flock members in the tropics have large territories, which would allow individuals to follow one another for long distances before one came to the edge of its territory and had to turn back. Moreover, many pairs could join each other at one spot

in the tropical forest because many species are present. It is likely that many tropical birds seldom interrupt flock-following to visit their nests. Certainly ant-tanagers of both species made few visits to their nests per hour (2 or 3 while feeding young), and it is well known that the size of tropical broods is generally smaller than that of northern broods (e.g., Lack, 1947. *Ibis*, 89:302–352). There may also be more nonterritorial species, more nonbreeding vagrants, and more nonbreeding immatures in tropical than in temperate forests. Some ant-tanager pairs were accompanied by one to three first-year birds, some greenlet territorial groups were trios rather than pairs, and many Dot-winged Antwren (*Microrhopias quixensis*) groups were larger than three birds.

Red-crowned Ant-Tanagers occasionally left a flock, visited their nests or engaged in territorial disputes or other activities for varying lengths of time, and later returned. At times one ant-tanager pair was replaced by a second after a territorial dispute when the flock crossed the ant-tanagers' territorial boundary. A wandering flock containing such birds as ant-tanagers must constantly vary in its composition.

I wish to thank the Belize Estates and Produce Company for their help at their Gallon Jug Camp, the National Science Foundation for fellowships supporting my studies, R. J. Newman of the Museum of Zoology at Louisiana State University for critical review of the manuscript, and G. H. Lowery, Jr., of that Museum, for directing the study.—Edwin Willis, *Museum of Zoology, Louisiana State University, Baton Rouge, Louisiana, May 6, 1959.*

Encounters between Barn Swallows and a Mockingbird.—On two occasions during June, 1958, I observed repeated attacks by Barn Swallows (*Hirundo rustica*) upon a Mockingbird (*Mimus polyglottos*). My home in Bethesda, Maryland, backs on a large golf course where Barn Swallows fly back and forth catching food, and where Mockingbirds nest in the bordering shrubs. (I know of no nesting site of the Barn Swallow within a half mile.) It is only when it is raining that the two species meet, for the swallows sit out the rain preening on a telephone wire which is within the territory of a nesting pair of Mockingbirds.

On June 25 my attention was drawn to several swallows which were making repeated dives on a lone Mockingbird sitting on the wire. I do not know which species arrived first. The Mockingbird attempted to thwart the attacks by directing a head-forward thrust at each diving swallow, and by snapping its bill violently. This action continued for several minutes, during which it appeared that the swallows never actually hit the mocker in their dives.

A similar encounter took place the following day. On this occasion swallows were sitting together on the same wire when a Mockingbird flew to a spot about 5 feet farther along, a place which it had used as a song post throughout the breeding season. The swallows left the wire, chattering, and began diving at the larger bird as before. This time the attack was well-coordinated, the seven swallows diving alternately, one from the east side of the wire, the next from the west. This forced the Mockingbird to turn completely around after each dive in order to thwart the next. Its defense was the same as before, and after several minutes of attacking, the swallows left to join others on a wire about 100 feet away. On other occasions I have observed Barn Swallows peacefully sharing the same telephone line with various species, at least seven in all, without the slightest sign of conflict.

These events bear a striking similarity to those described by Cross (1950. *Wilson Bull.*, 62:39). He observed five Barn Swallows making repeated diving attacks on a Loggerhead Shrike (*Lanius ludovicianus*) perched on a wire. Since it was well past nesting

period, he suggested that the swallows recognized the shrike as a predator (either by instinct or experience or a combination of both), and therefore attacked it. If the Barn Swallow recognized the shrike by obvious "sign stimuli" (e.g., dark body, white wing patches, white outer tail feathers, sitting alone on a wire in the open), could it be that the swallows reported above "mistook" the Mockingbird for the similarly-patterned shrike, and therefore attacked it?—JACK P. HAILMAN, *4401 Gladwyne Drive, Bethesda, Maryland, March 17, 1959.*

Common Grackle heavily infested with Mallophaga.— The number of Mallophaga (chewing lice) harbored by individual birds varies considerably even within the same host species. Of many factors limiting population size of the lice, preening by the host is undoubtedly instrumental in removing many lice and their eggs. A female Common Grackle (*Quiscalus quiscula*) (No. 55–A, KSCP), collected January 18, 1959, in Cherokee County, Kansas, was found to be carrying the unusually high number of 323 lice (*Menacanthus*). The bird appears to be normal except for a markedly malformed bill. The upper portion of the distal half of the lower mandible is lacking; the upper mandible is twisted, with irregular tomia and with an elongate horny growth at the tip. A V-shaped gap, 5mm. wide distally, separates the two mandibles for about half their length. When the bird was collected, a great number of mallophagan eggs still adhered to barbs of the under-wing coverts.

Our search for Mallophaga on 130 birds (representing 7 orders, 20 families, 44 species) collected in southeast Kansas during several winter months has revealed that many individual hosts are louse-free. Of those infested, most harbored less than 20 lice and only three were infested with more than 100 lice. Heavy lice infestation in the instance mentioned herein may be due primarily to the inability of the host to preen itself efficiently.—J. C. JOHNSON, JR. AND CHARLES A. LONG, *Department of Biological Science, Kansas State College, Pittsburg, Kansas, April 23, 1959.*

ORNITHOLOGICAL NEWS

Anyone writing to the Wilson Ornithological Society in general, or to any of its officers specifically, is urged not to address the University of Kansas, as is too frequently done, but to refer to the proper address as listed on the inside front and back covers of the *Bulletin*.

The Wilson Ornithological Society's new Endowment Committee Chairman is Dr. Richard Zusi, Coburn Hall, Department of Zoology, University of Maine, Orono, Maine. He replaces Dr. Olin Sewall Pettingill, Jr., who recently resigned the chairmanship.

The A. O. U. Council at the 1959 meetings in Regina authorized issuance of the first grants for research from the income of the Josselyn Van Tyne Memorial Fund. A sum of approximately $600 will become available at the end of the fiscal year, July 31, 1960. The Council assigned to the Research Committee of the A. O. U. the administering of these grants and it is hoped that the first recipient or recipients may be announced at the next A. O. U. meeting in Ann Arbor in August.

Any student of birds who has a special need for equipment, travel, assistance, or materials to further his research is invited to submit an application (10 duplicate copies) for a portion or all of the money available. This application should give a full description of the proposed research, the type of help that is required, when the money should be made available, the background and training of the applicant, and other pertinent information. The applications will be evaluated and rated by the Research Committee to determine how the funds will be allotted.

All applications for grants must be in the hands of the chairman not later than June 1, 1960. Send them to Dr. S. C. Kendeigh, Chairman, Vivarium Building, University of Illinois, Wright and Healey Streets, Champaign, Illinois.

JOSSELYN VAN TYNE MEMORIAL LIBRARY

The following gifts have been recently received . From:

H. Lewis Batts, Jr.—1 pamphlet
Charles T. Black—1 reprint
William H. Burt—1 reprint
Robert S. Butsch—1 book
F. G. Cooch—1 reprint
W. P. and B. D. Cottrille—11 journals
Kai Curry-Lindahl—2 books, 14 reprints
Jack P. Hailman— 4 reprints
Karl W. Haller—2 books, 1 pamphlet
Fr. Haverschmidt—3 reprints
Leon Kelso—2 translations
William Lunk—1 book
University of Michigan Museum of Zoology —1 occasional paper
D. F. Owen—1 pamphlet, 6 reprints
William H. Phelps and William H. Phelps, Jr.—1 pamphlet, 3 reprints
Allan R. Phillips—4 reprints
Robert Leo Smith—5 reprints
Peter Stettenheim—2 books, 2 reprints, 1 translation
Robert W. Storer—1 reprint
Harrison B. Tordoff—1 journal
University of Utah Dept. of Zoology and Entomology—3 reprints, 1 pamphlet
Mrs. Josselyn Van Tyne—110 books
David K. Wetherbee—2 reprints
Harriet B. Woolfenden—1 book, 23 colored prints of bird paintings by Fenwick Lansdowne

ORNITHOLOGICAL LITERATURE

Complete Field Guide to American Wildlife/East, Central and North/Covering All Species of Birds, Mammals, Reptiles, Amphibians, Food and Game Fishes, Seashells, and the Principal Marine Invertebrates Occurring Annually in North America East of the Rockies and North of the 37th Parallel. By Henry Hill Collins, Jr. Illustrated by Russell Francis Peterson, Nina L. Williams, and John Cameron Yrizarry. Harper & Brothers, New York, 1959: 7½x4½ in., xx+683 pp., maps, 200 figs., 48 color plates. $6.95 (de luxe edition, $7.95).

The title of this book, like an insurance policy, must be read in its entirety to be comprehended, and even then it leaves some doubt as to the book's scope. This work is, in truth, a field guide, with suitably small dimensions and strong binding, but its completeness is a matter of opinion, and its coverage is actually limited to selected groups of animals in eastern United States and Canada, west to and including the Black Hills and other eastern foothills of the Rockies, south to the borders of the Carolinas and Oklahoma, and north to and including the delta of the Mackenzie River and western Greenland. In all, 1439 animal species (author's count) are covered: first the birds, 454 species in 252 pages, well over a third of the book; then the mammals, 192 species in 88 pages; reptiles, 98 species in 70 pages; amphibians, 76 in 40 pages; fishes, 342 in 109 pages; and marine invertebrates, 277 in 99 pages.

Though four people, serving as an Editorial Advisory Board, "helped guide the plan of the work" and "read the manuscript in their respective fields," Mr. Collins wrote the book himself. How successful he has been in compiling his material, only the book's field use will tell. What interests us here are the organization and contents of the section on birds.

The introduction to this contains general information on the biology, history, ecology, and classification of birds and on some of the techniques of bird watching. All in all the information is appropriate, although the author has sometimes overstated matters (for example: "Being warm-bodied, birds can fly across the North Pole" (p. 4); bird watching is "a hobby of many millions of persons" (p. 5)), or has given misleading interpretations ("the food a bird eats is determined by the kind of a bill it has" (p. 7); species are arranged "in the presumed order of evolution" (p. 11)). Toward the end of the introduction he has outlined at length some of the activities and methods among bird watchers. Unfortunately, his treatment is so superficial as to make some of the aspects of bird watching seem foolish.

The bulk of the bird section comprises accounts of the species. Each adheres to a set pattern. After its title, consisting of common and scientific names, comes an introductory our-only-bird statement, a means to quick identification employed with discretion by Allan D. Cruickshank in his "Pocket Guide to the Birds" but used here as often as possible and at times carelessly. On page 22, the Gannet is said to be "our only large white sea bird with broad black wingtips" while on the same page, showing black on the tips of the wings, is a drawing of the White Pelican, a large white bird which frequents sea coasts. Again, on page 152, the Northern Three-toed Woodpecker is "Our only woodpecker with *a barred back and barred sides*," a statement that is hard to reconcile with a drawing on the same page of a Ladder-backed Woodpecker demonstrating very distinct barrings on the back and sides. Too many of the statements are loosely worded. The Western Kingbird (p. 154) does not have "*white outer tail feathers*" but outermost tail feathers edged with white; the Starling (p. 190) should have been referred to as a black bird instead of "blackbird."

Following the introductory statement comes information under subtitles, thus: Description, Habitat, Habits, Voice, Food, Nest, Eggs. The material is these categories is necessarily brief and, in the case of the first (Description), frequently marred by undefined terminology. Nowhere are "wing bars" and "eye rings" described or explained, nor are they shown on the drawing of the parts (topography) of the bird (Fig. 2); yet both terms are commonly used. In the accounts of the vireos, eye rings are used interchangeably with "spectacles" without any indication as to whether or not the terms are synonymous.

Toward the end of many species accounts is a subtitle, Age, under which is given the known maximum age. There are no additional figures to indicate *range* of known ages, or *number* of known ages. We are merely informed, for instance, that the Red-necked Grebe (p. 16) lives to 4 years and the Canada Goose (p. 33) to 22, the Arctic Tern (p. 127) to 22 years and the Roseate Tern (p. 128) to 10, the Robin (p. 180) to 10 years and the Eastern Bluebird (p. 183) to 4. While interesting, the figures can be misleading to the uncritical reader by giving him the idea that the Canada Goose usually lives five times longer than the Red-necked Grebe, and that there is a marked discrepancy in the ages of such closely related birds as the Arctic and Roseate Terns, or Robin and Eastern Bluebird, when we are actually not at all certain just how long these birds ordinarily live. Such data should either be qualified or left out entirely.

Each species account is concluded in a varied manner, sometimes with quotations from poets and naturalists, sometimes with comments on the habits of the species or its history. When a species' common name includes the name of a person, the conclusion is invariably devoted to identifying the person. In a field guide, whose text should be boiled down to bare essentials, the value of such extraneous material is questionable.

Greatly enhancing the species accounts are the range maps, one, sometimes two, to a species, worked out by Richard Ryan. They are carefully done, though one can find a few slips. The Horned Grebe is shown erroneously (p. 16) as breeding in northern New England, but this mistake is not as serious as the one in the accompanying text (same page) about the Horned Grebe "leaving for its Arctic breeding grounds." The map shows correctly that the species does not breed in the Arctic.

The bird illustrations comprise the drawings and silhouettes grouped in 51 figures and paintings in 28 color plates. All have been done by Russell Francis Peterson. It takes only a few moments for a person such as myself, who has regularly used Roger Tory Peterson's "A Field Guide to the Birds" (Second Edition, 1947), to discover that some of the drawings and silhouettes are, beyond a shadow of a doubt, copied from Peterson's work. Compare, for example, Figure 7 with the silhouettes on page 10 in Peterson, or the silhouette of the Turkey Vulture in Figure 26 with the silhouette of the same species on page 67. Here and there the artist has simply rearranged the subjects and made other minor alterations. A case in point is Figure 45, of the seven swallows on a sagging wire. In Peterson, page 162, there are six swallows in a different order from left to right, but posed in the same way, on a taut wire. Comparing the wash drawings of flying ducks in Figures 14, 15, 19, and 20 with similar wash drawings of the same birds in Peterson, one can readily surmise where the artist has obtained his ideas and some of his source material. He has taken pains to have all the ducks fly in the opposite direction.

The illustrations in color are amateurish in the extreme. If I felt that they represented a conscientious endeavor on the part of the artist to interpret birds as he has seen them in life or from specimems, I might say that he has mild promise; but I find too much evidence that he has relied to a large extent on other art work. It is hardly coincidence that his paintings on Plate 6 of the Great Blue Heron, American Bittern, and Green

Heron should show almost the same body attitudes and views as those depicted on Plates 14 and 15 by Don Eckelberry in Richard H. Pough's "Audubon Water Bird Guide." Interestingly, his painting of the male American Redstart with wings extended (Pl. 18) shows no orange-red on the bird's side (where the color should be), but on the bend of the wing where the color of the side often *appears to be* in paintings of the bird with wings folded.

When a new field guide to identification is published, we hopefully look for improvements that will more quickly point out distinctions. The bird section of this book has only one—a series of charts, by John Cameron Yrizarry, comparing closely related species. Otherwise we see what we have seen before in other guides, notably in the Peterson Field Guide Series—the same page makeup, the same use of boldface and italic type, range maps at the bottom of the pages as in Peterson-Mountfort-Hollom's "Field Guide to the Birds of Britain and Europe." Most of the drawings repeat the subjects depicted in other guides. As in Peterson's "A Field Guide to the Birds," there are drawings to show differences in the bills of three loons and two eiders, in the tails of the three jaegers and the four longspurs, and in the heads of two ptarmigan, and there are two color plates of fall warblers. The illustrations have one original feature—with most of the species are pictured their eggs.

Originality has not been the author's paramount objective. What he has strived to do, it seems to me, is to pull together between two covers as much material as possible from currently successful guides in the hope that his book will supplant all of them. In this effort he has overreached, at least insofar as the bird section is concerned, by assembling more material than can be handled consistently and conveniently in the space available. He has brought in and treated extensively a few Old World species (e.g., Ruff and Curlew Sandpiper) that occasionally show up in this country and many species that barely come within the established western limits of this book. He has omitted much-needed illustrations of such common species as the Acadian and Traill's Flycatchers. The Townsend's Warbler is illustrated, but the text account is omitted. Species are woefully jammed on the color plates, and the presence of their eggs makes the crowding seem even worse. Some surprising species are grouped together on the color plates. On Plate 27, which is captioned "BIRDS ONLY FOUND IN THE EAST," are the Greater Prairie Chicken, Ruff, Dickcissel, and Painted Bunting.

It is disturbing that a work with these shortcomings in its ornithological section should reach publication. But it has, and the fact that it has been brought out by a major publishing house will probably assure its wide promotion. If it should come into such wide demand as to require reprinting, I trust that the author and publisher will, in addition to correcting the factual matter in the text, give credit for the art work where credit is due.—Olin Sewall Pettingill, Jr.

Songs of Warblers of Eastern North America. Volume IV of the "Sounds of Nature" Series. Recorded by Donald J. Borror and William W. H. Gunn; narration by Thom Benson. Federation of Ontario Naturalists, 187 Highbourne Road, Toronto. $5.95.

Reproduced on this long-playing (33⅓ r.p.m.) record are 170 songs of 38 warbler species "known to breed regularly" in eastern North America. The species are grouped according to certain similarities of their songs, thus providing easier means of comparing them. In the case of all species at least two or three examples of songs (in the Magnolia Warbler, as many as 10) are given from different individuals, usually in widely separated parts of the species' range. This serves to point up the very considerable variation normally occurring within

species, while at the same time enabling the listener to attain greater familiarity with the vocal abilities of each species. Despite the many songs (more than 400) on the record, one may easily find the songs he wants to play by referring to the back of the album where there is a list of species and the number of the bands which have their songs.—Olin Sewall Pettingill, Jr.

A Bibliography of Birds. With Special Reference to Anatomy, Behavior, Biochemistry, Embryology, Pathology, Physiology, Genetics, Ecology, Aviculture, Economic Ornithology, Poultry Culture, Evolution, and Related Subjects. By Reuben Myron Strong. Publications of Field Museum of Natural History [now Chicago Natural History Museum], Zoological Series, Vol. 25, Part 4, pp. 1–85, 1959 (Finding Index). $2.75.

Parts 1 and 2 (Author Index) of Dr. Strong's widely used "Bibliography" were published in 1939 and Part 3 (Subject Index) in 1946. (For a review of all three volumes, see *The Wilson Bulletin* for 1947, vol. 59, pp. 49–50.) This, the fourth and final part (Finding Index), is a tool to assist in cross referencing. And a most welcome one it is!

From now on, almost anyone who uses the Bibliography will first consult the Finding Index, which consists of a "continuous alphabetically arranged list" of topics and names of bird species and groups of species occurring in the Subject Index. He will then go to the Subject Index which will in turn refer him to the Author Index. The vast majority of topics included in the Finding Index are anatomical, physiological, and geographical. Although many of them (for example, the eye) are already carried by special sections in the Subject Index, the Finding Index refers to these same topics in still other sections (in the case of the eye, 45 other sections). On looking through the Finding Index I was impressed with the large number of references to various bird species and groups of species, and also to geographical areas. I counted over 600 references to *Anas*, and 75 more references to 20 different species in the same genus. Geographical areas that I noted include all the continents (for example, Africa, to which there are 43 references) and many islands (Galapagos Islands, 10), as well as nations (France, 19), states (California, 22) and even cities (Chicago, 3).

The year 1926 marks the limit of literature covered by the Bibliography, but some references were added as late as 1938. To the modern investigator in ornithology, the Bibliography with its new Finding Index will be of invaluable assistance by facilitating a more thorough coverage of the earlier (and sometimes easily overlooked) books and papers.—Olin Sewall Pettingill, Jr.

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SUGGESTIONS TO AUTHORS

Manuscripts intended for publication in *The Wilson Bulletin* should be neatly typewritten, double-spaced, and on one side only of good quality white paper. Tables should be typed on separate sheets. Before preparing these, carefully consider whether the material is best presented in tabular form. Where the value of quantitative data can be enhanced by use of appropriate statistical methods, these should be used. Follow the A.O.U. Check-list (Fifth Edition, 1957) insofar as scientific names of United States and Canadian birds are concerned unless a satisfactory explanation is offered for doing otherwise. Use species names (binomials) unless specimens have actually been handled and subspecifically identified. Summaries of major papers should be brief but quotable. Where fewer than five papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited. Photographs for illustrations should be sharp, have good contrast, and be on glossy paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Authors are requested to return proof promptly. Extensive alterations in copy after the type has been set must be charged to the author.

A WORD TO MEMBERS

The Wilson Bulletin is not as large as we want it to be. It will become larger as funds for publication increase. The Society loses money, and the size of the *Bulletin* is cut down accordingly, each time a member fails to pay dues and is put on the "suspended list." Postage is used in notifying the printer of this suspension. More postage is used in notifying the member and urging him to pay his dues. When he does finally pay he must be reinstated in the mailing list and there is a printer's charge for this service. The *Bulletin* will become larger if members will make a point of paying their dues promptly.

NOTICE OF CHANGE OF ADDRESS

If your address changes, notify the Society immediately. Send your complete new address to the Treasurer, Merrill Wood, Dept. of Zoology and Entomology, Frear Laboratory, Pennsylvania State University, University Park, Pennsylvania. He will notify the printer.

1960 ANNUAL MEETING

The 1960 meeting of the Wilson Society will be held from Thursday to Sunday, May 5–8, at Gatlinburg, Tennessee. The host organization for this meeting will be the Knoxville Chapter of the Tennessee Ornithological Society, whose President, Mr. David Highbaugh, has written to the Secretary as follows:

"Mrs. Robert A. Monroe (1424 Tugaloo Drive, Knoxville 19, Tenn.) is our Local Chairman. Paul Pardue, President of the Tennessee Ornithological Society, and I are co-chairmen with Mrs. Monroe. The whole Knoxville Chapter makes up the balance of the committee. We are at your service."

Advance questions regarding details of the meeting (*other than accommodations*) should be addressed to Mrs. Monroe. Correspondence regarding *accommodations* should be addressed to: Mr. Tom Woods, Mgr., The Mountain View Hotel, Gatlinburg, Tenn. This will be the "headquarters" hotel, and its auditorium, the Huff House, will be used for papers sessions, etc. Mr. Woods suggests that members avail themselves of the hotel's European Plan rates (*without meals*), which range from $6.00 to $8.00 for a single room, and from $8.00 to $12.00 for a double room. Information on other accommodations is also available from Mr. Woods.

Program plans, so far, include a symposium on bird weights, to be led by Dr. Eugene Odum, who has suggested the tentative title: "The Ecological Significance of Bird Weights." The Secretary hopes that many ornithologists from the Southeast will plan to present papers at the meeting.

Those who have experienced a Wilson meeting at Gatlinburg, in Tennessee's Great Smoky Mountains, will need no urging to make immediate plans for attending the May 5–8, 1960, meeting there. Those who have not had that privilege should realize that it is difficult to visualize a more beautiful setting for a meeting—or a more delightful season for one—among hosts, moreover, who are anxious to show us their mountains, their birds, and their kindly hospitality.—A. M. B.